GEOGRAPHIC VARIATION IN SOCIAL BEHAVIOR AND IN ADAPTATIONS TO COMPETITION AMONG ANDEAN BIRDS

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Diglossa cyanea. This honeycreeper may be associated with either one or both of two specialized interspecific clusters in the Andes.

PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB, No. 18
Editor, Raymond A. Paynter, Jr.

GEOGRAPHIC VARIATION IN SOCIAL BEHAVIOR AND IN ADAPTATIONS TO COMPETITION AMONG ANDEAN BIRDS

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Published by the Club
1979

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1
INTRODUCTION

OBJECTIVES

The evolution of behavior is an important but difficult subject to study; it is more often discussed than analyzed. There are few historical or paleontological records of changes in behavior. Of necessity, therefore, students have usually had to rely upon inferential arguments derived from comparisons of patterns among living organisms. Two levels of comparison have been favored: (1) among individuals of a single species, and (2) among individuals of different species. At the first level, there has been a tendency to assume (in fact, if not in theory) that all members of the same species come from the same pool or source, an essentially uniform and continuous genetic and environmental matrix. At the second level, attention has usually been focused upon those behavior patterns that have been supposed to be "species specific" or "species typical." The term "typical" is loaded and can be misleading. Some patterns, e.g., some visual displays, do seem to be stereotyped, at least in form, in all or almost all members of a species of similar age, sex, and hormonal condition. Many other patterns are much more variable.

A principal objective of this paper will be to demonstrate that some kinds of social behavior may differ considerably among different populations of the same species, and that they tend to do so according to regular rules. There is geographic variation in behavior as in other characters. It will be suggested that comparisons among populations can provide information that is as useful as are comparisons among individuals or species. An attempt will be made to determine why the observed differences among populations occur. The search for causes will lead to a consideration of selection pressures; more precisely, to a consideration of the particular aspects of ecology and competition that might explain the pressures. Social behavior patterns can be advantageous in several ways. Some are adaptations to obtain necessary resources directly. Some are mechanisms to mediate, enforce, or evade competition for resources. Some are both.

Certain birds of the Andes have proved to be accessible to investigation along these lines. They also seem to be peculiarly revealing. They have provided the material for this study.

The higher reaches of the Andes have long been known to be interesting from a biogeographical point of view. Their habitats and biotas are marked by distinctive features (temperatures, endemic species, plant forms, etc.) that set them apart from the surrounding and adjacent lowlands. The northern third of the Andes is exceedingly complex in structure, with separate chains of mountains, cordilleras, and a scattering of single peaks and massifs (see accompanying map and comments). Many of the higher altitude areas and biotas are partly or very largely isolated from one another. In this respect they seem to be insular. They are not, however, like islands in oceans in all respects. Perhaps most notably, they are less impoverished in species. The statement is relative and approximate. Montane biotas certainly are less rich than those of the lowlands on the average. Numbers of species also change from place to place and habitat to habitat in the mountains. But it is still evident that most Andean areas have more or less diversified and "balanced" floras and faunas. They are inhabited by many organisms that have occupied most of the obvious "niches" or ecological roles and have exploited most of the available opportunities.

The balanced character of the biotas of the Andean "islands" must be due to a combination of factors. First, the separate cordilleras and massifs of the northern Andes are not too far apart, only a few kilometers in some cases. Second, the lowlands below the peaks are hospitable as well as rich. If nothing else, they are terrestrial. Lowland species may evolve new adaptations and be able to invade and settle in the highlands. This has occurred more frequently in some classes and orders than in others. For example, Andean birds are more distinctive, on the whole, than are Andean mammals. Among mammals, the carnivores are less distinctive than the ungulates or rodents. The correlations with size and trophic levels are obvious. A highland form may also be able to pass through the lowlands without great difficulty, even if it cannot survive indefinitely or reproduce there. (A highland bird flying from mountain to mountain may rest in a lowland tree, but a terrestrial bird flying from one oceanic island to another usually cannot rest on the water.)

Partly as a consequence of these features, it is possible, by careful inspection, to find almost precisely equivalent habitats and biotas, with similar diversities and ecological types, at many places in many regions of the Andes, even at very great distances from one another and in the isolated or semi-isolated chains and blocks. The Andean "islands" differ among themselves, sometimes appreciably, but all or most of them may have more similar ranges of environments than do most of their oceanic counterparts, such as the West Indies or the archipelagos of the southwest Pacific, where there are greater contrasts between high and low islands, volcanic islands and coral atolls, etc.

Thus the higher Andes are ideal for studies of some aspects of both behavioral and insular evolution. The effects of isolation, geographic variation, and adaptations to facilitate, accommodate, or repell invasions can be observed not only *in situ* but almost *per se*, clear of the distortions of extreme impoverishment and in conditions that are as nearly standardized as could reasonably be expected in the field. They should, therefore, be distinguishable with relative if not actual ease.

It is hoped that they have been distinguished to some point in the following pages.

MATERIALS AND METHODS

The Andean birds discussed in this paper belong to one or the other (in a few cases, both) of two series, or "clusters," of species: (1) Honeycreepers of the genus *Diglossa* and some of their relatives and competitors, and (2) some frequently associated tanagers, finches, warblers, honeycreepers, flycatchers, furnariids (*sensu lato*, including dendrocolaptines), woodpeckers, and others.

Many species of both clusters show pronounced *intra*specific, geographic variation in *inter*specific social behavior.

Partial and summary notes on the subject have already been published elsewhere (Moynihan, 1963a, 1968a, 1973). The details are presented here for the first time.

The data were gathered by personal observation in different parts of the Andes, from Venezuela to Bolivia, at irregular intervals between 1959 and 1974. The techniques used were straightforward. I simply walked through selected areas with binoculars and jotted down descriptions of the birds and their behavior as rapidly as I could. Photographs and sound recordings were made only for purposes of illustration and as aids to memory (the spectrograms will appear in a later paper). There was no collection of specimens. Most of the important species, with a few unfortunate exceptions, could be securely identified from published guides and museum skins.

SOME DEFINITIONS AND ASSUMPTIONS

Before proceeding further, it may be useful to define some terms and state some assumptions in order to clarify subsequent discussions and help to explain why certain topics are treated as they are.

The term "cluster" is perhaps the least awkward of possible alternatives. Here it is applied to any series or group of species that are connected among themselves, in one way or another, by the performance of real social responses of some appreciable strength or degree of specialization. "Cluster" does not, in itself, imply anything about ecology or competition or the nature of the responses involved. Nor does every species of a cluster have to respond to every other. (It is possible to find such situations as A reacting to B but not to C, while B reacts to C but not to A, and C reacts to both A and B or to neither, and all three species react to D, usually in different ways, etc. As some clusters include more than a dozen species, and many more in a few cases, the number of permutations can be very large.) The social boundaries of clusters are often slightly fuzzy. Some individuals and species can be half in and half out, and/or (as indicated above) belong to more than one cluster. In a few areas I found boundaries to be very vague indeed. This is not "typical." More often than not the usual contents of a cluster are fairly easy to recognize in practice. Most members tend to respond to other members noticeably more frequently or strongly than they do to nonmembers.

The term "cluster," as it is used here, must be distinguished from other usages and related concepts. It is not the same as the "cluster" of Cody (1974), which seems to be a synonym for "guild." The latter term is often applied to groups of (usually) overlapping or associated species of similar feeding habits. In this sense, it is incommensurable with cluster as defined above, although the cluster of *Diglossa* spp. also happens to be a guild in the conventional sense. The simple "constellation" of Diamond (1975) again has a slightly different meaning, but his "coadjusted constellation" may be nearly equivalent to cluster as used here. It would be used instead if it were not so cumbrous.

For various theoretical and practical reasons, the term "social" should apply to any and all reactions (except accidental) between or among individuals of the same or different species. The subsequent account will be primarily concerned with two kinds of behavior patterns: friendly gregarious responses and hostile (agonistic) responses, including attack, escape, avoidance, and inhibition or suppression. The two kinds of patterns should be considered equally social.

The term "competition" is also used in a very broad sense. One individual will be said to be competing with another when it appropriates, permanently or temporarily, a resource that would otherwise be available to (and quite possibly or probably utilized by) the other. Competition ranges from weak to strong. The loss of a competition may not be immediately very damaging, much less fatal, to the loser. Presumably it is always at least mildly deleterious insofar as it represents wasted effort and may entail further efforts to recover, or compensate for the loss of, expenditures of energy that could otherwise be, or have been, directed to some other worthwhile purpose. Energy is seldom in surplus. Thus, in the long run even the mildest competition must be serious to a group of individuals, a population, or a species. Only the length of the run will tend to increase with increasing mildness and to decrease with increasing severity.

Logic indicates that "competitive exclusion" (Hardin, 1960) must work. Obviously most members of Andean clusters are not excluding one another very rapidly. In fact, observations suggest that they are competing, but the competition among them seems to be mild to moderate, or rigidly controlled if strong, and less often direct (one to one) than what Diamond (1970) has called "diffuse." Diamond was discussing birds of New Guinea and adjacent islands. Diffuse competition may be more widespread or significant in the tropics than in the temperate zones. (See, also, below.) Food is usually the first resource to come to mind when competition is considered. Other resources such as resting places, lookout posts, protective cover, escape routes, nesting sites, and even time or opportunity to sing, would seem to be equally or more important for many Andean birds.

Several assumptions may be dubious or questionable but should still be accepted as appropriate, as working hypotheses, unless and until definitely disproved.

INTRODUCTION

The field biologist should assume that whatever exists is adaptive and advantageous on the whole—not necessarily the best adaptation possible but at least adequate. Existing phenomena are, after all, the results of long evolution. Some consequences flow from this assumption. Unless there is good evidence to the contrary, it should also be presumed that existing faunas are in equilibrium, neither unsaturated nor supersaturated. And, furthermore, that the patterns observed today are adaptations to present conditions. Of course, there probably are exceptions, but it is usually difficult or impossible to identify them with confidence. Historical explanations are attractive; I have used them myself, here and elsewhere. They are still methodologically dangerous. When they cannot be tested against hard data, as is often the case, they are much too facile. They can explain everything or, in effect, nothing of interest.

The term "isolation" as applied to islands is only convenient shorthand. No island is cut off from the world; all have been reached by some organisms. The Andean "islands" are less remote than many others. I have, therefore, implicitly assumed that they have been exposed to invasions by all suitable organisms. As usual in biogeographical studies, it is more often the absences than the presences that need to be accounted for.

ITINERARY

The specific regions visited in the course of this study, and the inclusive periods of observation in the field, are as follow:

Sierra de Mérida (western Venezuela).—15–27 September 1962. 3–13 April 1965. 28 August–5 September 1965.

Sierra Nevada de Santa Marta (northern Colombia).—12–17 August 1967.

Eastern Cordillera of Colombia.—28–30 September 1962. 22–28 October 1962. 15–27 April 1965. 20–26 August 1965. 7 September 1965. 29 August 1974. 6–7 September 1974.

Central Cordillera of Colombia.—21 October 1962. 1 November 1962. 8–25 May 1965. 17–20 July 1965. 27–29 July 1965. 1–6 August 1965. 14–18 August 1965. 29 March and 1 April 1972. 4–5 September 1974.

Northern End of the Western Cordillera of Colombia.—29 October–1 November 1962. 22–25 July 1965.

Southern Part of the Western Cordillera of Colombia.—2–6 November 1962. 2 March 1965. 29 April–7 May 1965. 26–29 May 1965. 6–13 August 1965.

Central Ecuador.—4–9 August 1959. 20 May–2 June 1960. 21–27 May 1961. 19–25 May 1962. 24–30 January 1964. 5–25 March 1966. 27–28 August 1974.

Northern Peru West of the Marañón.—8–14 February 1964.

Northern Peru East of the Marañón.—12–16 June 1966.

Central Peru.—1–9 April 1963. 1–5 February 1964. 21–28 May 1966. 13–17 August 1974.

Southern Peru.—10–13 April 1963. 16–23 February 1964. 31 May–8 June 1966. 17–23 May 1972. 19–20 August 1974.

Northern Bolivia.—14 October–3 November 1963. 26 February–12 March 1964.

ACKNOWLEDGMENTS

I am indebted to, and must sincerely thank, many persons and institutions. Olga F. Linares provided the habitat photographs, assistance in the field, and many stimulating ideas. W. John Smith and A. Stanley Rand gave advice on a series of problems, both technical and intellectual. William Rand and Donald Windsor were more than merely helpful with statistical analyses. Several of my colleagues at the Smithsonian Tropical Research Institute were kind enough to read and comment on drafts of this manuscript. Of course, I am solely responsible for the final conclusions and such errors as may remain.

The study was financed by the U.S. National Science Foundation (GB-1519) and the Smithsonian Tropical Research Institute. It was also facilitated in various ways by Humberto Alvarez L., Virgilio Angulo Matta, Enrique Borda Vallejos, J. I. Borrero H., Leonor Castellanos, the directors and personnel of the *Corporación del Valle del Cauca* and the *Corporación del Valle del Magdalena*, Eugene Eisenmann, Ricardo Escobar E., Adela Gómez, George B. Hill, H.-W. Koepcke, the late Maria Koepcke, Vicente Lehmann, Eduardo Moreno, the late Antonio Olivares, the late Williams H. Phelps, Sr., Eduardo Ruiz Landa, and Ana Judith Silva.

I am particularly grateful to the late F. C. Lehmann V. He shared his great wealth of information on Colombian birds and environments with me, and made my work in the country as pleasant as it was instructive. I should like to dedicate this paper to his memory.

2

BACKGROUND

Most of my observations in the Andes were made in humid areas between 2,400 and 3,700 meters above sealevel. This is the ''humid temperate zone'' of Chapman (1917 and 1926) and other early workers, but recent practice has been to employ other names for the region. It is cool on the average and even temperate in the ordinary sense of the word, but it differs from the so-called ''temperate'' zones of northern continents in other, more significant, respects. It shares many characteristics with the surrounding lowlands. There is comparatively little annual variation in either daylength or temperature. The Andean biota, distinct as it is, is more similar in composition to that of the lowlands than to those of North America or northern Eurasia. This must be partly a result of contiguity. One would not, in any case, have expected the climatic differences between highlands and lowlands to be more than a partial barrier or filter, as it seems to be generally true, at least for birds and mammals, that in the course of evolution it is easier to move from a continually hot to a continually cold environment, or vice versa, than from either place to environments of more variable temperatures, or again vice versa (see also Moynihan, 1971). Thus, Chapman's terms will not be used here. The habitats and biotas of the higher Andes will be called simply ''cold tropical.'' The particular zone on which I concentrated will be called ''humid cold tropical.''

The Andes have a complex geological history. Uplifting is supposed to have begun in some areas in the late Cretaceous, and to have proceeded and extended in several directions at various times during the Tertiary and Pleistocene. It seems unlikely that cold habitats or opportunities for cold-adapted biotas appeared much before the end of the Pliocene, after the uplift had achieved impressive proportions and climates had cooled over much of the world. With the onset of greater climatic fluctuations during the Pleistocene, the ranges of the local plants and animals must have shifted repeatedly, and expanded and contracted, at accelerated rates. There have been numerous publications on these subjects. An incomplete, but perhaps representative, list would include Ahlfeld, 1970; Bermúdez, 1969; Haffer, 1970; van der Hammen, 1961a, 1961b, 1972; van der Hammen and Gonzales, 1960; Hastenrath, 1967, 1971; Hester, 1966; Geel and van der Hammen, 1973; MacNeish, 1971; Putzer, 1968; Reichel-Dolmatoff, 1965; Salgado-Labourieau and Shubert, 1976; and Wilhelmy, 1957. The best summaries for biologists, with many additional references, are in Haffer, 1974, Simpson, 1975, and Simpson Vuilleumier, 1971.

The present distribution of cold humid climates in the tropical portion of the Andes is literally eccentric. Generally high humidity is characteristic

A diagrammatic sketch of the higher reaches of the central and northern Andes and other mountains mentioned in the text.

Areas above 2,000 m are shown in black and stipple. Black areas are generally humid and often suitable for the birds discussed in this study. Stippled areas are less humid or otherwise less suitable on the average. The distributions shown are greatly oversimplified, but the broad pattern is roughly correct.

The map extends from slightly north of 12°N to approximately 18°S, and from 84°W to 66°W. The scale of the northern part is 1:5,000,000. The scale of the southern part is 1:5,100,000.

The numbers indicate regions. 1 = the highlands of Costa Rica and Chiriquí (western Panama). 2 = Sierra Nevada de Santa Marta. 3 = Sierra de Mérida. 4 = western cordillera of Colombia. 5 = central cordillera of Colombia. 6 = eastern cordillera of Colombia. 7 = Ecuador. 8 = northern Peru. 9 = central Peru. 10 = southern Peru. 11 = northern Bolivia.

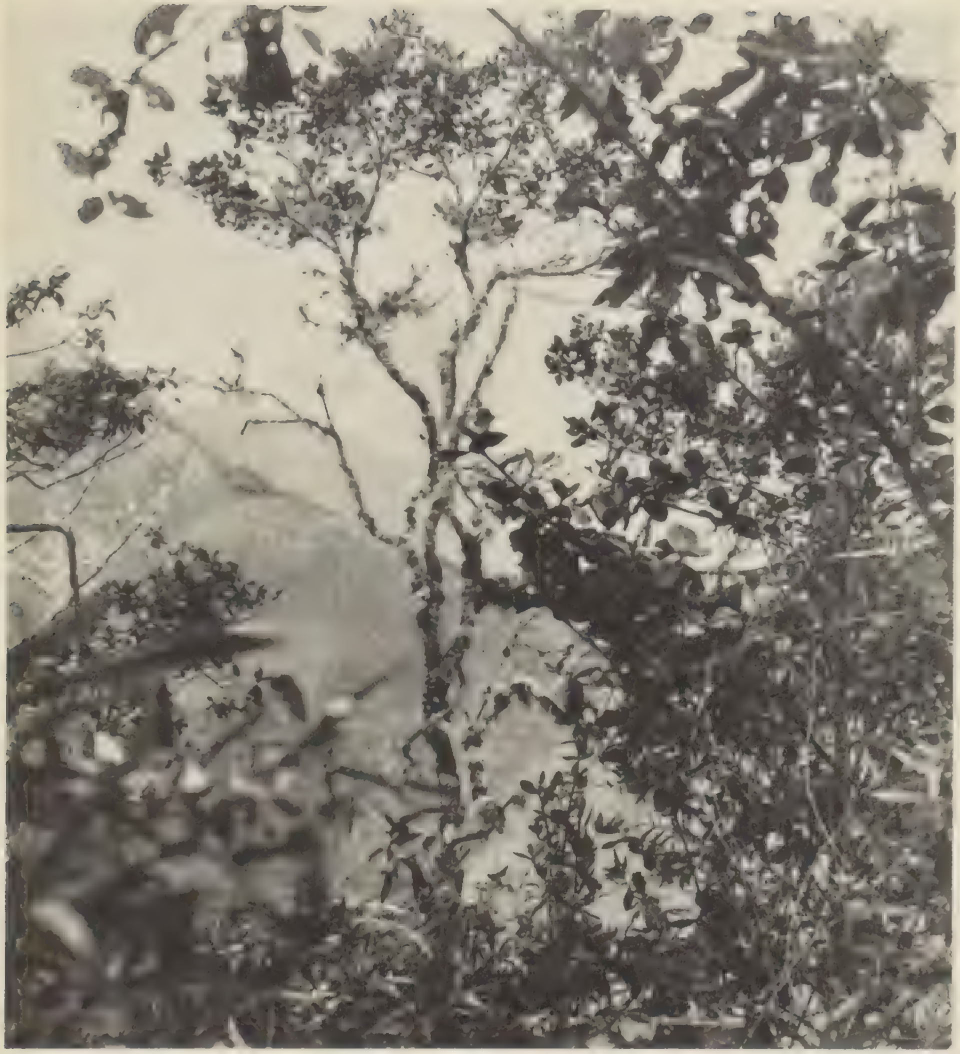

FIG. 1. A general view of natural or seminatural forest high on the eastern slopes of Machu Picchu, southern Peru.

This and the following photographs have been chosen to show several aspects of existing vegetation types in the humid cold zone of the Andes. They illustrate various forms, patterns, and densities of structures in forest, scrub, hedge and garden habitats. In the text there are notes on most of the sites.

All photographs by Olga F. Linares.

of most high altitude areas in Colombia and Venezuela. It reaches its average maximum in the western cordillera of Colombia (Pérez Arbeláez, 1954) and decreases to the south. The humid part of the cold zone fades to more arid conditions (see below) in the high basins and plateaus of central Ecuador, but it continues in strips along the slopes of the mountains bordering the

FIG. 2. Closeup of understory and edge vegetation, with ferns and bamboo, on the eastern slopes of Machu Picchu.

central mass of the Andes to the east and west. The western strip gradually disappears between southern Ecuador and central Peru (Koepcke, 1954 and 1961). The eastern strip goes farther down, to central Bolivia or slightly beyond. It is very irregular in shape, with many indentations on its eastern border created by the steep valleys of the affluents of the upper Amazon, such as the Marañón and the Urubamba. At its greatest extension in sub-Recent

Fig. 3. A hedge along the old road to Santo Domingo de los Colorados, central Ecuador.

times, it must always have been a series of linked peninsulas. This is indicated on Map 1, but only crudely.

The wind systems and some of the other climatic factors involved are summarized in Murphy (1936) and Schwabe (1968).

FIG. 4. Scrub on Guadalupe above Bogotá, eastern cordillera of Colombia. This sort of bush, with small, waxy, succulent leaves, is characteristic of the humid cold zone throughout the Andes and elsewhere.

There are many local differences within the zone. The relief of the Andes is so contorted that the total amounts of rainfall and fog or cloud may change over very short distances, a few hundreds of meters or less, even in regions that must be considered to be generally cold and humid throughout. There

FIG. 5. Yellow-flowered *Abutilon* in a garden in the small town of Silvia in the southern part of the central cordillera, east and north of Popayán, Colombia.

is a range from moist to sopping wet. The extreme limits may be much the same in most parts of the zone; but the merely damp is more common and (relatively) widespread in the south than in the north. This is what would be expected from the distribution outlined above.

Rainfall may also vary from month to month, sometimes considerably. The minor seasonal variations in temperature that do occur in the Andes, as elsewhere in the tropics, seem to depend upon fluctuations in humidity.

FIG. 6. Low scrub and edge vegetation on Guadalupe above Bogotá, eastern cordillera of Colombia.

The timing, onset, and duration of breeding by local birds may be causally related to rainfall, probably in different ways for different species and in different places.

Both breeding and nonbreeding birds were observed in all the areas visited more than once during this study.

With the existing climatic regime, and in the absence of human interference, the natural ''climax'' vegetation of most of the humid cold zone would be dense scrub and forest of varying height (see Cuatrecasas, 1958; Espinal and Montenegro, 1963; Weber, 1969; and Simpson, 1975). Second-growth and edge habitats presumably would be small and scattered around landslides and treefalls and along streams and torrents.

These undisturbed conditions are gone. They probably disappeared hundreds

FIG. 7. Scrub with large montane *Passiflora* bloom (center, seen in frontal view) along old road to Santo Domingo de los Colorados, central Ecuador.

or even thousands of years ago. Human interference has been significant for a very long time. The first paleo-Indian arrivals probably were responsible for the extinction of many "Pleistocene" mammals, including such large herbivores as mastodons and ground sloths (Martin, 1967). This, with its inevitable chain reactions, must have had profound effects upon the local

FIG. 8. A single *Colibri coruscans* in *Eucalyptus* (*globulus*?) tree in a garden, Silvia, central cordillera of Colombia.

ecology, perhaps affecting the numbers and distributions of particular plant species while conserving the general forest and scrub aspect. The later increase of human populations, and the appearance and elaboration of agriculture (see, for instance, Bennett and Bird, 1960; Lanning, 1967; and MacNeish,

FIG. 9. Bamboo (*Chusquea* sp.) thicket on Machu Picchu, southern Peru.

et al., 1975), must have produced other dramatic changes. Human populations declined after the Spanish conquest but again have built up to very high levels in many areas. As a result, the forest and scrub of these areas have been largely replaced by more open second-growth, hedges, gardens, crop fields, and pastures. Crops and types of cultivation can be shifted or rotated, regularly or irregularly. ''Natural-looking'' vegetation is now restricted to an intricate and partly discontinuous network of sites that have proved, for one reason or another, to be (so far) unexploitable or inaccessible to human settlement. It is still shrinking. As partial compensation, however, new patches of lush vegetation, in some ways comparable to natural forest and scrub, are being established in previously unsuitable areas with the spread of irrigation.

FIG. 10. Second-growth vegetation, with bamboo and treeferns, around patch of natural-looking older forest, Carpish Pass, central Peru.

A superficial "microinsularity" has been imposed upon the large scale insularity and "peninsularity" of the Andes as a whole.

Some examples of vegetation types are shown in Figures 1–10.

I tried to observe birds in both "natural-looking" and obviously artificial habitats. Fortunately, many of the species with which I was concerned are adapted to second-growth, edge, and other vegetation of similar structure. Their numbers probably are increasing under present conditions. They were not usually difficult to find or follow.

The humid cold zone is bounded by three kinds of distinctly different environments within the Andes. Vertically it extends from the lower limits of "alpine" moor and grassland, páramo and puna, down to lower altitudes where the vegetation begins to assume the aspect of the lowlands (the so-called "subtropical" zone of older authors). Horizontally in many areas, especially to the south, it adjoins arid or semiarid country.

The biological boundary or frontier with páramo or puna is usually abrupt.

The transition between high altitude and low altitude forests can be smooth and gradual where the continuity has not been broken by man (Terborgh, 1971). The boundaries with the arid zones are diverse. They are abrupt in some places, gradual in others, and sometimes with interdigitations or checkerboard patterns; the irrigation mentioned above has added another complication.

I made supplemental observations for comparison in some of these adjacent environments: in the páramo and puna of many regions; in semiarid areas around 3,000–3,300 m, mostly in Ecuador and Peru; and at both wet and dry sites at considerably lower elevations, mostly in Venezuela and Colombia. I also took a look at *Polylepis* woods in Peru. These peculiar plant formations occur at extremely high altitudes, well up into what is usually the zone of open moor and grassland. They are rather different from conventional forests, but they are inhabited by some birds that are related to those of lower elevations.

Perhaps the two most important points to be remembered from this sketchy survey of the Andean background is that the birds of the humid cold zone live in varied, variable, changing, and shifting habitats, and that they are potentially exposed, with greater or lesser probabilities, to invasions by animals of several other life zones and ways of life.

It will be seen that their behavior reflects these circumstances.

3

DESCRIPTION OF THE DIGLOSSA CLUSTER

GENERAL AND SYSTEMATIC

Members of the genus *Diglossa* are sometimes given the English vernacular name of "flower-piercers." This is hardly euphonious. It is better to use the Latin name as the common one.

Diglossas are small birds that feed on insects, nectar, and, in some cases, fruit. Some of their adaptations to obtain nectar are diagnostic of the genus. They have bills of unique shape. The lower mandible is thin, of moderate length, slightly upturned, and sharply pointed. The upper mandible is longer, also upturned, but with a sharp downward hook at the tip. Together they form an efficient tool for grasping and piercing the corollas of long tubular flowers from the side. The base of the corolla is held by the hook of the upper mandible while an incision is made by the lower mandible (Skutch, 1954; Moynihan, 1963a). Nectar, with or without small insects which may have drowned in it, is then sucked or lapped up by the U-shaped and brushy tongue (Vuilleumier, 1969). The great advantage of this mechanism is that it enables the diglossas to "tap" long tubular flowers that would not otherwise be manageable or useful to them, and would instead be reserved for birds with longer bills. Most flowers are not seriously damaged in the process. They are only marked by small slits. The openings are persistent, however, a fact which is not without consequences for many species of the local community, perhaps including the plants (see below).

Some diglossas attack small fruits by a variation of the flower-piercing technique. A fruit is plucked, impaled on the lower mandible, held by the upper mandible, and the juice and pulp are extracted by rapid movements of the tongue.

Other methods of feeding are less remarkable. All diglossas obtain insects by gleaning, more often on leaves than on branches. Some also chase insects in the air by "flycatching." All forms get nectar from flowers with short corollas by direct approaches from the front or top, putting the bill to the food without making an incision.

The genus is montane. It extends from the mountains of southern Mexico through the massifs of Central America, and from the flat-topped plateaus of the Guiana highlands (the "Pantepui" of Mayr and Phelps, 1967), the coastal hills of Venezuela, and the Sierra Nevada de Santa Marta along the major chains of the Andes to the ends of humid environments in Peru and Bolivia, and even beyond in a few cases. In the Andes it occupies the whole of the humid cold zone and extends some distance into lower country, although apparently never to the real lowlands, and into some semiarid areas. Different species and populations have different distributions within this range, but they all prefer forest (especially near the edge), scrub, hedges, and/or gardens. They may pass over or through pastures and crop fields, but they usually do not linger there.

Diglossas belong to the vast assemblage of "nine-primaried" songbirds (Oscines) that also includes the New World warblers, tanagers, American blackbirds and other icterids, Old World buntings and New World sparrows, cardinal and cardueline finches, etc. (see comments and review in Sibley, 1970). All honeycreepers are sometimes placed in a single subgroup, variously called Coerebidae, Coerebinae, Coerebini. The subgroup may be heterogeneous. My impression is that among honeycreepers, diglossas are most closely related, phylogenetically, to the conebills, *Conirostrum*, "*Ateleodacnis*," and *Oreomanes*, and to the Bananaquit, *Coereba* (Moynihan, 1968b). This would not preclude special relationships to other genera, even some which are not honeycreepers or have not been recognized as such (e.g., *Acanthidops*).

There are many kinds of diglossas. The genus would appear to be undergoing rapid change and perhaps proliferation. It is evident, nevertheless, that the numerous forms can be assigned to a few species or superspecies. Studies by Zimmer (especially 1929) and Hellmayr (1935) settled most of the outstanding systematic problems. Their results are embodied in the classifications of de Schauensee (1966) and Storer (1970). Vuilleumier (1969) has proposed a slightly different arrangement that is refined at some levels, but also complicated. For the purpose of the behavioral descriptions and analyses set out below, I shall use the simpler system (with minor modifications), postponing further comments on classification to another publication.

de Schauensee (1966) recognizes eight species in the main parts of the Andes, excluding pantepui and the coastal foothills of Venezuela. These are *D. coerulescens, cyanea, indigotica, glauca, baritula, albilatera, carbonaria,* and *lafresnayii*. They can be distinguished and categorized as follows.

Four species are largely blue, i.e., *coerulescens, cyanea, indigotica, and glauca*. They tend to have comparatively unexaggerated (less curved) bills, and used to be put in a separate genus *Diglossopis* (this may be retained as a subgeneric name, when and if desirable). They also are sexually monomorphic and show little geographic variation in appearance. *D. coerulescens* is rather dull gray-blue, noticeably lighter on the breast and belly, with some black around the eyes and on the lores. *D. cyanea* is a brighter blue, with a more extensive black facial "mask" and a lighter blue "cap" on the crown and nape, that often appears to be almost white in the field. Both are rather slender-bodied and have moderately long tails. *D. indigotica* is even brighter than *cyanea*, but with little black on the face. It looks plump, stubby, and short-tailed. *D. glauca* is generally dull and dark; I have not seen it in the field. *D. cyanea* and *coerulescens* are broadly sympatric at higher elevations throughout many of the humid parts of the northern and central Andes. *D. indigotica* is most characteristic of lower elevations on the western slopes of the Andes in Colombia and Ecuador. *D. glauca* has a discontinuous distribution along the eastern slopes at similar altitudes.

The other four species, or species-groups, might be loosely termed "black and brown." They show the diglossa-type bill in more or less extreme form. Two of them are sexually dimorphic. In *D. albilatera* adult males are blackish, with conspicuous white axillary patches, while females are brown. This species usually occurs at moderate elevations and/or in particularly humid areas in the northern Andes, Ecuador, and parts of northern Peru. It does not extend farther south. Nor does it show much geographic variation in morphological characters. The forms that have been included in *D. baritula* are more varied and extend from Mexico to Bolivia and Argentina. Females are olivish everywhere. Adult males are always primarily dark gray or blue-gray (slatey) above. Males of the northern populations from Mexico to Honduras (nominate *baritula* and closely related races) and all the South American races (*sittoides*, etc.) are buffy below. Rather surprisingly, the adult males of the geographically intermediate populations of Costa Rica and Panama (*plumbea*) are gray below, and appear in the field to be uniformly slatey all over. The South American forms usually occur at moderate elevations in areas of less than maximum humidity. (I observed *plumbea* in the province of Chiriquí in western Panama on several occasions in September 1958, March 1959, and March 1960. The habitat preferences of this population seem to be rather different from those of its South American relatives. The difference is discussed below.)

The remaining two species, or species-groups, *carbonaria* and *lafresnayii*, show many similarities to one another. With one possible exception (again see below), all populations of both species are sexually monomorphic in plumage. Adults usually are black or blackish, in some cases variegated with patches or stripes of white, rufous, light gray, and/or gray–blue. Both species extend from Venezuela to Bolivia. *D. lafresnayii* tends to be most abundant just below the lower limits of páramo and puna; *carbonaria* tends to be most abundant a few hundred meters lower.

D. carbonaria has six main forms: (1) *gloriosa* is in the Sierra de Mérida, Venezuela. Typical adults of this form are black above, the black covering the whole head and spreading over the throat, and rufous or buffy on the rest of the underparts, with some gray on the rump and conspicuous light gray-blue humeral patches. (2) *nocticolor* is on the slopes of Sierra Nevada de Santa Marta. The adults of this form are black with gray on the rump. (3) *brunneiventris* is a series of populations of extremely discontinuous distribution, in the northern parts of the western and central cordilleras of Colombia, most of the Andes of Peru, and parts of northern Bolivia. Adults are black above, rufous below, with gray on the rump, gray–blue humeral patches, black throats, and rufous malar or "moustachial" stripes separating the black of the throat from the black of the rest of the head. (The forms *gloriosa* and *brunneiventris* would appear to intergrade. Some individuals in the Sierra de Mérida, which should be *gloriosa*, have traces of the malar stripes of *brunneiventris*.) (4) *humeralis* is on the eastern cordillera of Colombia. Adults of both sexes are black with gray on the rump and gray-blue humeral patches. (5) *aterrima* is the form of the southern part of the central cordillera of Colombia, perhaps the southern part of the western cordillera, and the central Andes from southern Colombia (Nariño) through Ecuador to the northernmost part of Peru, north and west of the valley of the upper Marañón. Adult males are entirely black. Some females that appear to be mated to adult males are generally dull medium gray, resembling juveniles (de Schauensee, 1966; Moynihan, 1963a). They may, of course, become as black as the adult males later in life. (6) Nominate *carbonaria* is the form of the eastern slopes of the Andes of Bolivia, south and southwest of the range of southern *brunneiventris*. Adults of both sexes are mostly black above, with gray on the rump, gray-blue humeral patches, gray breast and belly (streaked or mottled with black), and rufous undertail coverts.

D. lafresnayii includes (1) Nominate *lafresnayii* which is widely distributed in the Sierra de Mérida, the eastern and central cordilleras of Colombia, and the Andes of Ecuador and northern Peru north of the upper Marañón. Adults are black with gray-blue humeral patches. (2) *gloriosissima* is in the western cordillera of Colombia. It has black on the head, throat, and upperparts, rufous below, with blue-gray humeral patches. (3) *unicincta* is of northern Peru, south and east of the upper Marañón. Adults are black, with rufous undertail coverts, some dark gray on the rump, and very reduced humeral patches (both the latter features are inconspicuous in the wild). They also have white malar stripes and a prominent pectoral band. This band is pure rufous in some museum specimens. In all of the relatively few individuals observed in the field in the course of this study, the band was "double," i.e., rufous in front along the border of the black throat and white behind. (4) *pectoralis* is from central Peru south of the valley of the Huallaga River and, like *unicincta*, always has considerable white in the pectoral band. (5) *albilinea*, of southern Peru, is black with dark gray on the rump, only slightly reduced gray-blue humeral patches, rufous undertail coverts, and whitish malar stripes, often tinged with rufous toward the rear border. (6) *mystacalis* is in northern Bolivia. It is black with dark gray rump, well-developed humeral patches, rufous malar stripes, and rufous undertail coverts.

D. albilatera, D. baritula, and *D. carbonaria* are particularly small and rather "chunky." *D. lafresnayii* is less diminutive, and seems to differ in proportions among its races. Some races appear to be much larger-headed than others, probably because they have longer feathers on the crown and nape.

Conebills of the genus *Conirostrum* also have proliferated in the Andes. At least one series of forms pertains to the diglossa social cluster. Other taxa are more closely linked to other associations, but may impinge upon diglossas indirectly or intermittently. All have thin, short, sharp bills without hooks, but resemble the smallest diglossas in other respects. They can be divided among a number of taxa, perhaps 6–7 species and 4–5 superspecies.

The better known forms are *cinereum, rufum, ferrugineiventre, sitticolor*, and *albifrons*. The numerous populations that have been assigned to *cinereum* extend from the cordilleras of Colombia to Bolivia and even northern Chile. *C. rufum* has a rather restricted range on the Sierra Nevada de Santa Marta and in the eastern cordillera of Colombia. *C. ferrugineiventre* occurs from central Peru south to northern or central Bolivia. A recently discovered species, *tamarugensis*, seems to be confined to a small area of northern Chile (Johnson and Millie, 1972); it is the only species of montane conebill that I did not see in the course of this study. All these forms appear to be closely related to one another. They are all largely gray or blue-gray above and more or less extensively buffy or rufous below. *C. rufum*, *ferrugineiventre*, and *tamarugensis* are essentially morphologically uniform throughout their limited ranges. There is more morphological variation in the *C. cinereum* group affecting both general size and tone of underparts, but most of the differences are inconspicuous to a human observer in the field. *C. sitticolor* ranges from Venezuela to Bolivia and is more vividly colored. In adult plumage the head is largely black, with bright blue postocular stripes and blue on the throat in some populations; the back is bright blue; the wings are blue and black; and most of the underparts are bright orange-rufous. The geographic variation in head pattern does not seem to play a significant role in the behavior discussed in this paper. *C. rufum*, *ferrugineiventre*, *sitticolor*, and most races of *cinereum* occur at relatively high altitudes in the cold humid or semihumid zones in forest, scrub, and/or gardens.

The remaining montane forms, conventionally assigned to *C. albifrons*, also range from Venezuela to Bolivia. They are even more distinctive than *C. sitticolor*. They are characteristic of forests at somewhat lower altitudes. Unlike other conebills they show extreme sexual dimorphism in plumage. Adult males are largely black. In the northern Andes the black is washed with glossy purplish-blue on the back, rump, and wing coverts. This blue diminishes in populations toward the south. In most areas adult males also have bright purplish-blue caps. These do not fade out to the south. All the blue-capped forms used to be placed in a separate species, *atrocyaneum*. Adult males of the mountains of Venezuela and the eastern and central cordilleras of Colombia, viz. *C. a. cyanonotum*, *C. a. centralandium* and nominate *albifrons*, have white instead of blue caps. In both cases, at a distance the adult males look more like species of blue diglossas rather than conebills. Adult females of all populations are largely greenish with blue on the head. Their plumage is reminiscent of some kinds of *Dacnis*, lowland honeycreepers which might not be expected to be particularly closely related. Perhaps the systematic position of *C. albifrons* needs to be reassessed.

Species of other groups that may affect diglossas, most notably some hummingbirds and finches, are described below in the accounts of different regions.

The scientific names cited above will be used "without prejudice," even though some of the forms may be assigned different ranks in future revisions. Only a few abbreviations or paraphrases will be employed in certain contexts. All the South American forms of the *D. baritula* group will be called "*sittoides*," in contradistinction to *plumbea* of southern Central America and the remaining "*baritula*" of northern Central America and Mexico. Similarly, all the forms of the *C. albifrons* group which have blue-capped males will be called "*atrocyaneum*" to distinguish them, as a separate category, from the rather different "*albifrons*" types. The populations subsumed under such terms as "*sittoides*" and "*atrocyaneum*" do behave, in some ways, as if they were good species.

VARIATIONS IN INTERSPECIFIC BEHAVIOR

Many species of the diglossa cluster show considerable geographic variation in several kinds of social behavior. The differences described in this section of the paper are the ones that characterize the cluster as such. They are differences in interspecific hostile, negative, aversive behavior.

The extent and nature of this variation may be revealed by describing the social situation in each region separately. Most of the regional accounts will cover or touch on several topics, viz., the kinds of diglossas seen, other species belonging to the cluster, still other relevant species, areas and habitats visited, ecological preferences of species observed, territorial relations, interspecific fighting and/or avoidance, inhibition of "song," and miscellaneous comments.

It will be convenient to begin by presenting two extreme cases in central Ecuador and the southern part of the western cordillera of Colombia, to proceed to describe intermediate situations in other parts of the northern Andes, and then to survey the southern populations of Peru and Bolivia.

Some theoretical aspects or implications of the behavior described will be considered in connection with the first extreme cases. Others will be reserved for the next sections of the paper.

Central Ecuador

Forms of diglossas seen: *D. cyanea*, *D. indigotica*, *D. carbonaria aterrima*, nominate *D. lafresnayii*, and *D. albilatera*. Other members of the cluster include a form of the *Conirostrum cinereum* group and the warbler *Myioborus melanocephalus*.[1]

Several brush-finches of the genus *Atlapetes* appear to be on the verge of the cluster. These are certainly *A. rufinucha*, one or more members of the *A. schistaceus* species-group, and perhaps *A. pallidinucha* as well. Other relevant species are hummingbirds such as *Aglaeactis cupripennis*, *Colibri coruscans*, at least one kind of *Eriocnemis* (probably *vestitus*), perhaps *Lesbia nuna*, and many others.

Like diglossa, and even more than whitestarts, brush-finches tend to develop local forms. *Atlapetes schistaceus* belongs to a widespread species-group (the *A. schistaceus* species-group) that extends from western Venezuela to

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[1] Birds of the latter genus have been called "redstarts" in English, as they are supposed to be related to the common North American "Redstart," *Setophaga ruticilla*. It might be better to call them "whitestarts." Their tails or "starts" are marked with white, not red. *M. melanocephalus*, the two forms usually assigned to *M. ornatus*, *M. flavivertex* of the Sierra Nevada de Santa Marta, and even *M. torquatus* of Central America are a rather tightly knit group, perhaps no more than a superspecies. They all behave in similar ways and seem to fill similar niches.

southern Peru. The group has been revised in detail by Paynter (1972). He recognizes six species and many subspecies. Some species have similar plumage patterns, and might be difficult to distinguish in the field under unfavorable conditions. Some of them also have similar or parallel habitat preferences. As far as I could tell, the birds that I encountered in most regions of the Andes were examples of *A. schistaceus*, except in central Ecuador where the form seen most frequently was *A. l. leucopterus*.

Relations among *D. cyanea*, *D. carbonaria aterrima*, *D. l. lafresnayii*, and *C. cinereum* in and around Quito and some nearby areas, e.g., Nono, San Juan, and other sites on the slopes of Pichincha and Atacazo, have been described in Moynihan (1963a). Although each species has its habitat preferences, there is wide overlapping of ranges in this region. Individuals of *D. l. lafresnayii* occur not only in the dense bush at the borders of páramo but also down to 2,300–2,400 m in forest and scrub, especially in very humid areas.

D. carbonaria aterrima is very abundant around 2,300–2,400 m, but also occurs higher and lower, up as far as the highest *D. l. lafresnayii* at some points and in gardens and more scattered vegetation at a variety of altitudes.

D. cyanea and *C. cinereum* occur in many of the same areas as *D. carbonaria aterrima* and *D. l. lafresnayii*. All four species can be found both in bushes and in trees.

D. cyanea moves and perches in trees rather more frequently than do the other diglossas seen; it may also tend to go higher in trees.

C. cinereum enters somewhat drier and more open habitats than most of the diglossas, even *D. carbonaria aterrima*. But none of the differences is great enough to be a real barrier.

The four species are sympatric and even occur at precisely the same sites in the Quito region. Each mated pair or adult male (and possibly also single adult females?) of each species defends its territory against conspecific pairs and individuals, but the territories of different species are often widely or completely overlapping. Different species often use the same routes and visit exactly the same spots. They do more. They search for, find, and catch insects and other small invertebrates on many of the same leaves and twigs, and feed on many of the same flowers. They must, therefore, be competing strongly with one another. It is also obvious, since they are surviving together, that the competition must be partly mitigated. The overlaps are never quite complete. This is as true of feeding as of habitat preferences. The various species do not feed on the same things with absolutely identical frequencies. The many insects and flowers that are taken or tapped by the local nectarivores are seldom equally attractive or available to all of them. More often than not, one kind of bird devotes more effort to one kind of flower or insect than to another, while a second species does the reverse.

The competition is also "canalized," confined or diverted, by timing. In the Quito region the different diglossas and *C. cinereum* seldom attempt to use the same routes, perches, or foods simultaneously. Individuals of different species tend to keep apart from one another by at least 2–3 meters and often much more, even when their territories are almost identical. They usually do this with little or no overt fighting. They simply avoid one another. An individual of one species is reluctant to approach a perch or a flower occupied by another species and/or an individual of one species leaves a perch or a flower well before another species approaches. They share the same space and many of the same resources by refraining from contact.

The clues by which this behavior is mediated are inconspicuous to a human observer. My impression is that individuals simply express certain states of motivation, such as hunger, by slight movements and intention movements. Neighbors seem to be on the lookout for hints, and usually interpret them correctly.

Avoidance is complemented by control of "songs"—vocal advertising displays. Individuals of the same species often sing partly or wholly synchronously. Individuals of different species seldom do so, but instead tend to alternate their songs. This must be due to reciprocal inhibition of song among the various species, an inhibition precisely parallel to their spatial arrangements.

Thus, in the Quito region different species are kept apart by an *elaborate system of social segregation.*

In 1964 and 1966 I worked over a wider range of sites than during earlier visits to Ecuador. I made observations along both the inner and outer slopes of the mountains bordering the central plateaus (or high intermontane valleys) to the east, in and around the towns of Papallacta, Pifo, and Guápulo, and farther along the road to Santo Domingo, well below San Juan, on the western slopes of the mountains to the west. In the latter area I came across a few *D. albilatera* in humid habitats at 2,750–2,650 m. As far as I could tell, they interacted among themselves and with other members of the cluster in the same ways as the other diglossas of the region.

Interactions between the honeycreepers of central Ecuador and the local whitestarts and brush-finches are less clear-cut and more difficult to describe. Although taxonomically a warbler, *Myioborus melanocephalus* gets much of its food by flycatching. Individuals of the species constantly flutter up from trees and bushes to chase insects in the air. They are erratic and acrobatic. They also are members of mixed flocks with which diglossas and *C. cinereum* have ambivalent relations (see below). It is almost impossible, therefore, to determine if they are "consciously" trying to avoid approaches to or by the honeycreepers. They certainly manage to do so, by indirect if not direct mechanisms on many occasions. The brush-finches tend to remain low and skulking in thick vegetation. Possibly they also avoid or are avoided by some or all diglossas, but I did not see them clearly often enough to be sure of this. The relationships of whitestarts and *Atlapetes* spp. to the cluster are revealed by their singing. The whitestarts participate fully in the inhibition of song system. Their songs are as rarely synchronous with those of diglossas and *C. cinereum* as the latter are with one another. The brush-finches are less well integrated or more careless, but their songs are less frequently interfered with or drowned out by vocalizations of diglossas than might be expected by chance alone. There is even some evidence that in the absence of diglossas there is mutual inhibition between whitestarts and brush-finches, as well as among different species of *Atlapetes.*

The reciprocal inhibition of song is both real and partly independent of the structures of the patterns involved. All the local species sing very frequently during the breeding season and some, e.g., *D. cyanea,* may breed twice a year. Thus the birds must have to be careful to avoid overlapping songs. It is also pertinent that the songs of different species of the cluster are strikingly different in form. (The vocal repertories of some other nine-primaried oscines are described, with references, in Moynihan, 1962a, 1962b, 1963b, and 1966. The repertories of most species are strictly comparable and largely homologous throughout. Different species have, however, selected different components for inclusion or emphasis in advertising performances. The diglossas illustrate this phenomenon as well as or better than any other group.) The songs of *D. albilatera* are brief trills or rattles. Those of *D. l. lafresnayii,* and also of *Myioborus melanocephalus* and *M. ornatus,* are longer and rather melodious twitters. They are rather similar to one another in general aural effect, but usually distinguishable in the field by details of form. The songs of *D. c. aterrima* and *D. cyanea* are more rapid twitters. Those of *D. cyanea* often have distinctive introductory notes, while those of *D. c. aterrima* may incorporate trill or rattle phrases. The vocalizations of the local population of *C. cinereum* are diverse; some patterns that may function as song are twittering, reminiscent of *D. c. aterrima;* others are series of accelerated "zee" notes. The song-like patterns of *Atlapetes* spp. are melodious whistles or "plaintive notes." Most of the brush-finches also utter twitters or rattles as "greetings."

Members of the diglossa cluster do not simply react to the songs of other species that are most like their own. Some of the songs involved in the reciprocal inhibition system are at least as different from one another as any of them is from songs of some other species that are not in the system. Conversely, some songs that are not in the system are quite similar to some of those that are. For instance, all the species of the diglossa cluster of central Ecuador seem to ignore the songs of Andean Sparrows, *Zonotrichia capensis.* These sparrows are abundant in many areas where diglossas and their social partners are found. They are noisy. Their songs are similar to and partly homologous with those of *Atlapetes.* (The songs of some Argentinean populations of *Z. capensis* are described in Nottebohm, 1969. Both behavior and morphology would suggest that *Zonotrichia* and *Atlapetes* are closely related phylogenetically.) But the members of the local diglossa cluster have never been observed to react vocally to the sparrows. They appear to sing or refrain from singing with *Zonotrichia* "at random." Andean Sparrows do not seem to be significant to Ecuadorean diglossas, although they may impinge upon related forms in at least one other region (see below).

Visual resemblances are equally unnecessary. Not only are some of the diglossas and *C. cinereum* different from one another in color, but both *Myioborus* spp. and *Atlapetes* spp. have distinctive patterns of their own, with much yellow on the whitestarts and some of the brush-finches, and very different and characteristic shapes. The finches are also conspicuously larger than the others.

Some *Atlapetes* compete with other species of the cluster for food as well as other resources. They take a variety of small invertebrates, picking them off leaves and twigs and from the ground. *A. rufinucha* was seen to eat flowers and flower buds of plants that provide nectar for the honeycreepers.

Many or most of the birds that are not involved in reciprocal inhibition of song are also independent of the mutual avoidance system. They approach or are approached by members of the diglossa cluster quite freely, in some cases with appreciable frequency.

Avoidance and inhibition seem to be adaptations to regulate both interspecific resource competition and its possible social consequences. Both kinds of regulations are important. They are connected but disparate. One kind does not necessarily reinforce the other.

The effects of avoidance and inhibition on competition must depend in part upon the circumstances in which they occur. The relative numbers of individuals of different species in an area may be the most relevant circumstance. It is conceivable that avoidance and inhibition, especially the former, may reduce competition, simply by slowing down interactions, when the numbers of individuals of different species are approximately equal. This is speculative. It is more nearly certain that the two systems, and perhaps especially inhibition, will tend to accentuate or accelerate competition when the numbers are very unequal. An individual of a rare form in the cluster must not only observe the traffic (avoidance) rules, but it will also inevitably encounter difficulties in advertising by song (if male) or finding an advertisor (if female). The inhibition is interspecific, not intraspecific. These difficulties may increase disproportionately with a decreasing population. It seems very likely that a species of the cluster that is declining for some other reason(s) will be pushed farther along the path to local extinction by the purely social problem of communication.

The same problem must confront any rare scouts or pioneers of an invading species—if they are prepared to play by the rules. I do not know if they should be expected to be prepared or not. Perhaps, if they are close relatives, and therefore probably the most dangerous competitors, they might already be adapted to the same or similar systems. If not, there are other advantages to the systems, temporary but nonetheless tempting, that might induce conformity. They flow from the smoothing over of other difficulties.

Avoidance and inhibition must have meliorative effects on an immediate and superficial level. They must help to "civilize" competition, to keep it within what might be called "decent" bounds. They discourage fights and other alarms and excursions, and prevent or minimize confusion of messages. An individual of a rare species may be allowed to transmit clearly on the few occasions when it is allowed to transmit at all. It may be suppressed or excluded in the end, but only "politely."

In or by themselves, the meliorative effects must be beneficial to all the individuals affected. Doubtless this is one of the reasons why avoidance and inhibition have evolved and persisted in some regions, why there has not been greater selection pressure in favor of rogues or outlaws that break the rules. Presumably, whenever competition occurs and the competitive struggle cannot be won easily and promptly, there should be definite advantages for all involved to making the struggle as conventional and painless as possible. This goal might be achieved by any one of several different methods. As will be described later, other Andean birds have evolved methods different from those of members of the diglossa cluster. But the techniques of the diglossas of central Ecuador work well enough.

They do not always work perfectly. Both avoidance and inhibition break down occasionally. They can do so during encounters between any of the members of the cluster. In central Ecuador breakdowns seem to be most frequent when *Atlapetes* or hummingbirds (see below) are involved, but they also occur among the honeycreepers themselves.

These lapses are suggestive. Even among the integral members of the cluster, leaving aside the marginal brush-finches and hummingbirds, there are some forms that contribute more to the maintenance of the systems than do others. In central Ecuador *D. c. aterrima* seems to be the most important contributor. It is one of the most widely distributed forms in terms of altitudinal and habitat tolerances. It resembles every one of the other members in some aspect of appearance or voice. The other members of the cluster probably interact with it more frequently than with any other species. Breakdowns of the inhibition and avoidance systems are sometimes conspicuous in areas where *D. c. aterrima* is rare or absent, or during periods when it is relatively quiet and undemonstrative. Around Nono in January of 1964, for instance, *D. cyanea* was in breeding condition, very active, and in full display, while *D. c. aterrima* was subdued, skulking, and apparently not breeding. At this time and place, *D. cyanea* made an unusually large number of "mistakes," interfering with the songs of several other species and even attacking or supplanting them. *D. c. aterrima* is not essential; the avoidance and inhibition systems can work without it. But it may function as both buffer and model.

Some of these variations also suggest that maintenance of the systems is partly dependent upon practice. There is further evidence to the same effect. At dawn, when songs are just beginning, reciprocal inhibition is often muddled. It improves later in the morning when most of the participants are singing most frequently. This may be another indication of the specialization of the system. Reciprocal inhibition deteriorates toward the middle of the day when songs gradually fall off.

Other forms of diglossas and conebills must occur in central Ecuador. It has already been mentioned that two diglossas, *D. glauca* and *D. indigotica*, are characteristic of altitudes lower than those at which I worked. I never saw *D. glauca*. I did see a single *D. indigotica* once on Atacazo in an area thickly populated by *D. l. lafresnayii* and *D. c. aterrima*. It did not interact noticeably with any bird. Two other forms, *D. coerulescens* and *D. baritula* *"sittoides,"* have been found at higher altitudes in central Ecuador, but I missed them. *D. coerulescens* is rare in several regions. It may be subdued by the more abundant and generally successful *D. cyanea* (see below). Perhaps I overlooked it in Ecuador by chance or inadvertence. *D. b. "sittoides,"* on the other hand, is common in many parts of the Andes. Chapman (1926) collected specimens at several of the Ecuadorean sites that I visited. Perhaps in recent years the species has become rarer in this region. It may be particularly vulnerable to competition from *D. c. aterrima, C. cinereum,* and/or hummingbirds.

Possibly the reciprocal inhibition and avoidance systems cannot accommodate more than a limited number of species. I saw several individuals of *C. sitticolor* in central Ecuador. They were associates of mixed flocks and not members of the diglossa cluster. This seems to be true of the species throughout its range. I did not see any *C. albifrons "atrocyaneum."* Some populations of the same species or superspecies in other regions resemble *C. sitticolor* in their social proclivities. I shall not, therefore, mention either of these kinds of conebills further in this section of the paper. They will be noted later in connection with flocking.

Hummingbirds, as well as diglossas and conebills, also feed on nectar and small arthropods. Their physical adaptations to nectar feeding are more extreme than those of any honeycreepers, and they are exceedingly abundant and diverse in the Andes (see, for instance, Greenewalt, 1960, and Grant and Grant, 1968). As a group they are strong competitors with all other nectarivorous birds. Unfortunately, I did not pay much attention to the hummingbirds of central Ecuador, partly because their overt interspecific reactions are rather surprisingly inconspicuous and unelaborate. My observations, such as they are, suggest that the territories of many hummingbirds overlap those of members of the local diglossa cluster, and that some species, at least *Aglaeactis cupripennis, Colibri coruscans, Lesbia nuna,* and *Eriocnemis vestitus,* usually avoid or are avoided by diglossas and possibly some other members of the cluster. When approaches do occur, they are unmistakably hostile. The larger hummingbirds, e.g., *Colibri* and *Aglaeactis,* are usually but not always the aggressors. It is remarkable, however, that fights between hummingbirds and diglossas seem to be much rarer in central Ecuador than in some other regions of the Andes.

Most of the Ecuadorean hummingbirds were quiet while I watched them. *Colibri coruscans* was the exception. Males of this species repeat short simple song phrases for days or weeks on end when they are in reproductive condition. Ecuadorean *C. coruscans* showed some slight, but only intermittent, indications of a reciprocal song inhibition relationship with members of the diglossa cluster, including whitestarts and brush-finches. Presumably they could not conform more often or consistently because their song system, being what it is, cannot support the frequent pauses that more effective inhibition would entail.

(A disclaimer may be inserted here. Some montane hummingbirds are nomadic or make regular altitudinal migrations. I observed the behavior of

Andean species only *vis à vis* honeycreepers or mixed flocks. Some of them may behave differently at other times in other areas.)

Southern Part of the Western Cordillera of Colombia

Forms of diglossas seen: *D. cyanea*, *D. coerulescens*, *D. albilatera*, and a form of either *D. carbonaria* or *D. lafresnayii* (probably *D. c. aterrima* or an intergrade between it and *D. c. brunneiventris*). Other obviously relevant species are: the whitestarts *Myioborus ornatus* and *M. miniatus*, the hummingbirds *Colibri coruscans*, *Coeligena torquata*, and *Heliangelus exortis*. Possibly also some *Atlapetes*, at least *rufinucha* and *schistaceus*.

Most of my observations of the birds of this region were made on or near Cerro Munchique west of Popayán. They extended from the finca "La Carpintería" near the base of the mountain, ca. 2,390 m, to the summit, just below 3,000 m, and to an area called La Palma, ca. 2,540 m, on another and smaller mountain even farther west. (Some of the local people refer to this last site as San Gerardo, but the name may not be official.) Briefer visits were made to the Farallones range, in and around the field station of the *Corporación del Valle del Cauca* that bears the exotic name of "Korea," 2,550–2,800 m, and near the town of Uribe, ca. 2,550 m.

The surroundings of La Carpintería are flower gardens, pastures (some with hedges), and young second-growth forest and scrub. There is more natural-looking vegetation above the farm. The upper slopes of Munchique are, or were at the time, largely covered by high and very humid forest with lush undergrowth, interrupted by sparser and lower bush on recent landslides. At the very top of the mountain, the tall forest is replaced by equally dense but shorter "alpine" forest or scrub, culminating in a cleared area (with police, radio, and television relay stations!). The Farollones are similar to Munchique in many ways. They have tall forest at the moderate altitudes where I did most of my work. The neighborhood or Uribe has a larger human population and consequently a more varied array of habitats, both highly artificial and seminatural.

The western cordillera averages lower than most other parts of the Andes, and is broken into more separate blocks. It is this topography, combined with the prevailing winds, that explains the extreme humidity of the region already noted above. Areas of sopping wet conditions seem to be more predominant in this chain, and areas of merely damp less common or extensive, than in other regions visited.

The abundant diglossas of the southern part of the chain are *cyanea* and *albilatera*. Both were seen at most bush, scrub, and forest sites, but not (perhaps significantly) in the flower gardens at La Carpintería. *D. cyanea* prefers trees. It sometimes goes as high as 15 or more meters above ground and comes down to low vegetation only relatively infrequently. Local *D. albilatera*, by contrast, prefers bushes and low tangles, usually 0.5 5 meters above ground. It is most common in the wettest areas and in the undergrowth of forests or along the almost impenetrable edges of paths within forests.

Each preference is fairly typical of its respective species. The contrast between the species, however, is particularly noticeable in the southern part of the western cordillera where *D. cyanea* is more consistently arboreal than elsewhere. Of course, there are many more trees to choose among. Forests are more extensive and have survived better in this excessively humid region than in some others. Thus, even though the territories of the two diglossas are broadly or completely overlapping, literally as well as figuratively, almost throughout the region, the two species may not have too many opportunities to come into close contact with one another. When such opportunities do appear, however, the two forms tend to avoid one another more or less carefully.

As would be expected, obvious breakdowns also occur from time to time. They are least rare at moderate altitudes, ca. 2,400–2,500 m. Vegetation is particularly dense in some areas at these altitudes and may, therefore, provide more cover to permit or encourage a certain amount of adventurousness. Most of the occasional breakdowns are due to *cyanea* rather than *albilatera. D. cyanea* descends to low bushes more frequently at moderate altitudes than at higher ones in this region. The difference seems to be ''intrinsic,'' not a simple consequence of crowding or some similar parameter. Populations of *cyanea* can be equally large or small at both high and moderate altitudes. This behavior may be another indication, like some of the reactions of individuals at Nono, that *cyanea* is less rigidly fixed into the diglossa cluster than are some other species. This, in turn, may help to explain how or why *cyanea* can also fit into other clusters such as mixed flocks (see below).

A third species, *coerulescens*, is much less abundant than either *cyanea* or *albilatera* in the southern part of the western cordillera of Colombia, but is certainly more visible here than in central Ecuador. I saw individuals and pairs of *coerulescens* in the alpine vegetation at the top of Munchique and in ''pseudoalpine'' scrub and forest stunted by the wind in a pass between peaks at ca. 2,500 m at La Palma. Their territories overlapped those of both *cyanea* and *albilatera. D. coerulescens* seems to prefer the highest levels of the available vegetation. This means that it was partially separated from sympatric *albilatera* in the same way as was *cyanea*. The vertical separation was not very great, however, as the alpine and pseudoalpine scrub was not very tall and was appreciably shorter than some of the forests inhabited by *cyanea* at other and lower sites. I did not see any face-to-face encounters between individuals of *albilatera* and *coerulescens*. Thus, when and if they were not kept apart by their preferences for different heights and kinds of vegetation, they must have been segregated by purely social mechanisms like those of most of the diglossas and *C. cinereum* of central Ecuador. I did not see any close encounters between *coerulescens* and *cyanea* either. Their segregation must have been entirely due to social avoidance. Individuals of the two species certainly fed and perched in many of the same places but never, during my observations, at the same times. It is interesting that the two species were able to maintain such a delicate balance in the absence of a variety of other forms, especially *D. carbonaria.*

The ecological differences between *cyanea* and *coerulescens* are clearer in the southern part of the western cordillera of Colombia than in any other region explored in detail. They may be worth summarizing briefly, even at the cost of some recapitulation. Both species could be described as primarily arboreal, but *coerulescens* seems to be confined to "dwarf" forest at high altitudes or to vegetation of similar structure at somewhat lower altitudes in peculiar edaphic conditions, while *cyanea* ranges through the same habitats and taller and richer vegetation at lower altitudes as well. Both species have comparatively large territories. (Blue diglossas and *Conirostrum cinereum* tend to have larger territories than black and brown diglossas almost everywhere.) Neither *D. cyanea* nor *D. coerulescens* is as frequently nectarivorous as some of their relatives. Both spend a lot of time gleaning insects from leaves. *D. cyanea* visits flowers in the southern part of the western cordillera of Colombia and elsewhere. It also takes small fruits in other regions. *D. coerulescens* was not seen in the western cordillera to feed by any method besides gleaning, although it does visit some flowers, including exotic eucalypts, on occasion in other parts of the Andes. It seems likely, in fact, that *coerulescens* is even less frequently nectarivorous than *cyanea*. It has the least specialized bill of all diglossas (see illustrations in Vuilleumier, 1969).

There is reciprocal inhibition of song among the three species of diglossa in the southern part of the western cordillera of Colombia. It usually works very well. As in central Ecuador, it does not depend upon morphological resemblances between the songs themselves. The rattles of *D. albilatera* are quite different from the twitters of *D. cyanea* here as elsewhere. The songs of *D. coerulescens,* on the other hand, are rather similar to those of *D. cyanea.* Again, the *cyanea–coerulescens* relationship must be difficult, as different individuals of the local *cyanea* population are not hesitant to sing simultaneously, overlapping or interrupting one another in full flow.

There is reciprocal inhibition of song among the diglossas, at least between *D. cyanea* and *D. albilatera* and the two whitestarts of the region, *Myioborus ornatus* and *M. miniatus.* This also works very well. It was most conspicuous at moderate altitudes in the Farallones in May of 1965. Three species, *D. cyanea, M. ornatus,* and *M. miniatus,* were all abundant, breeding, and highly vocal, but each was extremely careful not to interfere with the songs of the other two.

Some of the local *Atlapetes, A. rufinucha* and *A. schistaceus,* may adhere to the same inhibition system on occasion.

Relations between the diglossas and the local hummingbirds are obviously complex, probably more so than around Quito, perhaps partly because hummingbirds are even more common in the western cordillera of Colombia than in central Ecuador. Two of the species seen most frequently were *Coeligena torquata* and *Heliangelus exortis.* Both are fairly large and very aggressive. Their territories overlap in many areas. They fight with one another. Either species can be the aggressor. The aggressor usually wins, driving its opponent away temporarily. Both species also overlap the three local diglossas. The diglossas appear to try to avoid the more domineering hummingbirds. Nevertheless, I saw several attacks by *Coeligena torquata* on *D. albilatera* at the Farallones. And several more attacks on *albilatera* by another hummingbird, *Adelomyias melanogenys,* in the same general area. *D. albilatera* seems "to be low man on the totem pole" in this region. At the same time it provides valuable assistance to its oppressors. Among the favored sources of food for many diglossas throughout the Andes are the large, long, tubular, brightly colored (pink, red, or orange) flowers of the montane species of *Passiflora* (quite different from the familiar cultivated Passion Flower of lowland origin). The diglossas make incisions at the bases of the long corollas of these flowers in their usual way. Individuals of *albilatera* do so regularly in the southern part of the western cordillera, and their holes are visited frequently by *Coeligena torquata, Heliangelus,* and some other smaller, unidentified hummingbirds. *D. albilatera* is usually skulking and hidden during the visits. The hummingbirds put their bills to, and apparently through, the incisions. Presumably they are getting nectar of a kind that would not have been accessible to them in the absence of diglossas. Montane *Passiflora* flowers are too long and large for any of these particular hummingbirds to get much nectar by a direct frontal approach, and their own bills are unsuited to cutting. Thus the diglossas are, doubtless unwittingly, helping their competitors. Perhaps they cannot avoid doing so. It is also possible that they derive compensatory advantages. Perhaps predators are discouraged by an abundance of aggressive hummingbirds. If so, *D. albilatera* is not only helping its competitors and oppressors but also is being helped by them "in return."

Whether or not the plants are being helped is another question. They can hardly fail to be affected in some way, for good or for ill. The activities of the diglossas could have several results in addition to the infliction of minor injuries. They could expose the flowers to a greater range of actual or potential pollinators, allow or induce pollinators to change their tactics, reduce the supply of nectar and possibly pollen available to other species, and even alter the distributions and abundances of ectoparasites such as mites (see Colwell, 1973, for a discussion of these factors in another region).

The characteristic shape of montane *Passiflora* flowers may be an adaptation to climatic rather than biotic conditions (see the next section of this paper). The colors can only be designed to be attractive. As diglossas are among the animals most likely to be attracted, the obvious inference is that these honeycreepers probably do more good than harm to the plants.

Colibri coruscans is widespread in the southern part of the western cordillera of Colombia but not usually abundant, now, in most of the surviving natural habitats. It is, however, overwhelmingly dominant in the gardens of La Carpintería, so much so that very few other hummingbirds and no diglossas strayed into the gardens during my observations. This is all the more remarkable because the gardens were crowded with ornamental shrubs and other flowering plants, including red-flowered *Abutilon*, pink, red, purple, and white *Fuchsia*.

and orange *Kniphophora* that are attractive to diglossas in other parts of the Andes, such as the eastern and central cordilleras of Colombia. Local *C. coruscans* seems to have acquired a near monopoly of resources which other species would be expected to desire and to be capable of exploiting. They may maintain this monopoly by aggression. There were so few possible competitors in the gardens of La Carpintería that I could not study interspecific behavior *in situ*, but it may be significant that I saw several attacks by *C. coruscans* upon *D. albilatera* in adjacent woods.

The general situation is clear. Most of the nectarivorous members, or potential members, of the diglossa cluster of the southern part of the western cordillera of Colombia are *separated microgeographically* by restrictions to *different levels or kinds of vegetation*. Spatial segregation by individual avoidance is comparatively unimportant. Some of the microgeographical separation seems to be enforced by overt fighting. Some of it may be aftereffect of earlier fighting. Disputes may have accentuated or refined habitat preferences. Preferences and aggression can be synergistic in appropriate contexts.

Apparently as a result of these arrangements, there are fewer species of the diglossa cluster at any given point at any given time in this region than in equivalent environments in central Ecuador. (There may also be fewer species in the region as whole. This is not necessarily a consequence of the type of separation. See the account of northern Bolivia.)

The most noticeable gaps in the diglossa cluster of the southern part of the western cordillera are *D. carbonaria* and *D. lafresnayii*. One form of the latter species, *D. l. gloriosissima*, has been recorded from the "mountains west of Popayán" (Chapman, 1917). I did not hear or see anything like it in the region. I caught one brief glimpse of a single bird which could have been a form of *D. carbonaria* in sparse scrub on a landslide halfway up Munchique. There are other small areas on or near Munchique that appear (by comparison with other regions) to be suitable for one or both of these groups, but the areas may be too small and transitory to support populations of either in a healthy state for any appreciable length of time. If competition is the immediate or proximate cause of the absence or decline of the suppressed species, the operative agents could be or have been *D. albilatera*, *Colibri coruscans*, and/or other hummingbirds.

Sierra de Mérida

This is the first of the "intermediate" regions to be considered. The Sierra de Mérida is a geographical endpoint, but its inhabitants do not represent a social extreme. Relations among the members of the diglossa cluster, and their associates and rivals, are both more varied and more variable in the Sierra de Mérida than among the same or equivalent species in either central Ecuador or the southern part of the western cordillera of Colombia. They are also, therefore, more difficult to categorize or summarize briefly.

I worked over a very wide range of sites in Venezuela, including some unusually low ones. It may be worth describing some of the reactions of lower altitude birds for comparative reasons, for the light that they may throw upon the behavior of their higher altitude relatives and analogues. Thus the following account will be divided into two partly independent series of notes and comments.

Observations were made in and around the city of Mérida itself and in its suburbs, especially Chorros de Milla, ca. 1,640–1,700 m; on the nearby mountain of Pico Espejo (most frequently between the cable car stations known as La Montaña, 2,442 m, and La Aguada, 3,452 m, less frequently below the station at Loma Redonda, 4,095 m); along the borders of the more distant Páramo La Negra in Tachira to the east, ca. 2,600–2,800 m; and just below the Páramo Zumbador near the town of San Cristóbal to the west, ca. 2,700 m. Zumbador was visited in August of 1965. The other areas were surveyed more or less thoroughly during all visits to the region.

The Zumbador area is extremely humid, with extensive areas of alpine scrub and patches of cloud forest. The vegetation of Pico Espejo ranges from sparse alpine scrub to very rich "upper subtropical" forest. The areas visited at La Negra were largely scrub, interrupted by pastures and with a few groves of young second-growth trees. The city of Mérida and its suburbs are a mass of gardens, with many exotic and ornamental flowering shrubs and trees, surrounded by farms, pastures, sometimes with hedges, and abandoned fields in various stages of regeneration.

Birds of higher altitudes.—Forms of diglossas seen: *D. cyanea, D. coerulescens, D. carbonaria gloriosa, D. l. lafresnayii,* and *D. albilatera.* Other possibly or probably relevant species are: *Myioborus ornatus, M. miniatus, Atlapetes schistaceus, A. albofrenatus, Zonotrichia capensis,* and *Coeligena bonapartei.*

Birds of lower altitudes (the level of the city of Mérida and Chorros de Milla).—Forms of diglossas seen: *D. cyanea, D. carbonaria gloriosa, D. albilatera,* and *D. baritula "sittoides."* Other members of the cluster are: *Coereba flaveola,* the warbler *Vermivora peregrina* (see below). Another possibly relevant species is: *Colibri coruscans.*

It will be convenient to describe the social situation at higher altitudes first. *D. albilatera* is common and widespread. It predominates on the lower slopes of Pico Espejo and reaches the border of páramo at La Negra, perhaps also at Zumbador, in small numbers. As usual, it is most abundant in very humid areas where trees cover dense scrub and understory. It tends to stay low in the vegetation but may go up into trees to reach particularly attractive flowers. I saw individuals of *albilatera* go higher in trees, and do so more frequently, in the Sierra de Mérida than in the southern part of the western cordillera of Colombia. The local form of the *D. carbonaria* group, *gloriosa,* is common at La Negra and scattered on Espejo but was not seen at Zumbador. It prefers scrub, often semiopen, with little or no tree cover. *D. cyanea* is more evenly distributed. It is never as crowded together as are some clumps of *D. albilatera* and *D. c. gloriosa* (doubtless because of its larger territory), but occurs almost everywhere in the region at moderate densities. *D. coerulescens* is less abundant than any of the preceding forms. I did, however, see in the course of this study more individuals of the species at La Negra and Espejo than anywhere else in the Andes, except the eastern cordillera of the Andes. Both *D. cyanea* and *D. coerulescens* of the Sierra de Mérida are typically arboreal, although less exclusively in the tops of trees than their counterparts at Munchique.

D. l. lafresnayii was found only at Zumbador. W. H. Phelps, Sr. (pers. comm.) collected specimens of this form on Espejo some years ago, but the local population seemed to have gone by the time I arrived. At Zumbador *lafresnayii* was rather numerous and crowded along the edges of very dense forest and scrub, usually on western slopes (these slopes can be very cold in the mornings, and, of course, the species occurs at higher altitudes in some parts of the Andes). The only other diglossas seen or heard at Zumbador were a fair number of *cyanea* and perhaps one or two *albilatera*.

As far as I could tell, all the local diglossas feed in much the same ways as their closest relatives in other parts of the Andes. Different forms often take the same kinds of foods. Only two points or possible deviations may be noteworthy. *D. cyanea* of Espejo was seen to eat a lot of small fruits. The Sierra de Mérida is one of the (few) regions in which *D. coerulescens* was seen to visit flowers fairly frequently.

There is some degree of both microgeographical separation and social segregation among the diglossas of the Sierra de Mérida, but both are very obviously imperfect, apparently less effective than in central Ecuador or the southern part of the western cordillera of Colombia. The black and brown types are the ones that show microgeographical separation. In one way, *D. l. lafresnayii* of Zumbador is more isolated than any other population of the form that I studied. This is the only *lafresnayii* area in which some or many individuals do not overlap or adjoin individuals of the *D. carbonaria* group. *D. c. gloriosa* and *D. albilatera* are also largely separated from one another by their different habitat preferences, but their territories do overlap in intermediate and border habitats. The ecological relations among these birds may well be precarious. They are at least exceptional. *D. c. gloriosa* is relatively less abundant and widespread, or tolerant, than are the other forms of the *carbonaria* group in most of the Andes, and the local population of *D. l. lafresnayii* is also comparatively small and restricted. It might not take too much ecological change in the Sierra de Mérida to reduce or eliminate them both and produce a situation like that of Munchique. The blue diglossas are less confined than their black and brown colleagues. Territories of *D. cyanea* overlap those of all other species. *D. coerulescens* territories overlap those of *D. cyanea, D. albilatera*, and *D. c. gloriosa*. When territories of different species overlap, there is some mutual avoidance and reciprocal inhibition of song. Avoidance and inhibition are the rule in all cases, but they are often honored in the breach. I saw repeated attacks by *D. l. lafresnayii* upon *D. cyanea*, attacks by both *D. c. gloriosa* and *D. cyanea* on *D. coerulescens*, attacks by *D. coerulescens* on *D. c. gloriosa*, and face-to-face contacts without fighting between *D. l. lafresnayii* and *D. cyanea* and between *D. cyanea* and *D. albilatera* (once an *albilatera* actually followed a *cyanea* in an apparently friendly manner). I also heard many overlaps of songs between *D. l. lafresnayii* and *D. cyanea* and between the latter and *D. albilatera.*

Interactions between diglossas and some of the local hummingbirds convey the same impression of rather ill-natured muddle or slipshod control. One of the dominant hummingbirds of the Sierra de Mérida, especially at La Negra, is *Coeligena bonapartei.* Like related *Coeligena torquata,* it is very aggressive. Individuals of *bonapartei* fight among themselves, and they were seen to attack *D. cyanea, D. coerulescens,* and *D. c. gloriosa,* as well as *Colibri coruscans* and many smaller hummingbirds, probably including *Eriocnemis* types. Both *D. c. gloriosa* and *D. cyanea* were also seen to attack some of the same and possibly other small hummingbirds.

In the circumstances, it is remarkable that *Colibri coruscans* and the diglossas seem to ignore one another. Especially as the local population of *C. coruscans* occurs over a substantial range of altitudes and at many heights above ground in both bushes and trees. *Colibri coruscans* definitely is not a member of the diglossa cluster in these areas of the Sierra de Mérida. Much more surprisingly, *Zonotrichia capensis* appears to be more relevant. It may even be semi-integrated. I heard some sparrows alternate songs with *D. c. gloriosa* and also with *Atlapetes schistaceus* without audible overlaps. This is the only part of the Andes in which I noticed such arrangements. Perhaps competition is stronger between *Zonotrichia* and diglossas in the Sierra de Mérida than elsewhere. This possibility may be supported by some observations in and near the city itself (see below). *Myioborus ornatus* is common in many areas inhabited by diglossas in the region. *Myioborus miniatus* was observed on some of the lower slopes of Pico Espejo. This species is widespread in the mountains of the New World tropics (viz., the notes on the Farallones cited above). Throughout its range it tends to be more concentrated at lower altitudes than *M. ornatus* or the equivalents thereof, although some overlaps occur and may even be frequent. *Atlapetes schistaceus* is common in many of the higher stretches of the Sierra de Mérida. *Atlapetes albofrenatus* is abundant on Espejo. There is at least a trace of interspecific avoidance and inhibition among the whitestarts and brush-finches and between them and the local diglossas.

The typical nectarivorous birds of Mérida and its suburbs are many hummingbirds, including *Colibri coruscans, D. baritula "sittoides,"* and the Bananaquit, *Coereba flaveola.* They are found in all gardens, feeding on insects and a great diversity of flowers, including the brilliant red (vermilion) blossoms of a large and abundant *Erythrina,* purple and red *Bougainvillea,* and the whitish flowers of imported eucalypts. The population of Bananaquits is dense. Individuals and pairs of the species tend to have small territories and to be crowded together. Individuals of *D. baritula "sittoides"* are less abundant and have larger territories on the average. Much the same can be said of local *C. coruscans.* The territories of the three species are broadly or completely overlapping.

Another bird that visits flowers in the city quite frequently, in apparent search for nectar or pollen, is small, warbler- or conebill-like in shape and movements, obscurely colored, and olivish above with a light superciliary stripe. It is difficult to identify in the field, but it must, I think, be the warbler *Vermivora peregrina.* The species breeds in North America. Most individuals appear in Venezuela only in the nonbreeding season, essentially the northern hemisphere autumn and winter. Yet I certainly saw some during all my visits, even in April of 1965. Perhaps the birds seen at this time were getting ready to migrate. Or perhaps a section of the population fails to migrate on occasion. (There were individuals of other and more easily identifiable migrant species around during the same April.) Individuals of the presumed *V. peregrina* seem to be less common than Bananaquits or even *D. baritula "sittoides"* in and around Mérida, but not really rare. They may be rather sedentary in this environment. Their territories or home ranges overlap those of Bananaquits, *D. baritula "sittoides," and C. coruscans.*

All four species perch and feed in many of the same places. All are aggressive. Bananaquits fight among themselves and supplant, chase, and attack individuals of other species. They are also attacked by larger birds, most notably *Zonotrichia capensis.* (The sparrows of the gardens of Mérida investigate and probe into flowers, such as *Bougainvillea,* unusually frequently. I do not know what they are getting by this behavior—perhaps insects or buds—but their activities may reduce or change the amounts or kinds of foods available to other species.) Both *D. baritula "sittoides"* and the presumed *V. peregrina* show a fair amount of intraspecific hostility. Both may also attack miscellaneous small birds of other species, e.g., hummingbirds and flycatchers, but their attacks are seldom pressed home determinedly. Both apparently try to avoid approaches by Bananaquits and to keep out of the way of one another, but not always successfully. In several well-planted gardens, I saw Bananaquits dash at and actually peck *V. peregrina,* several *V. peregrina* and *D. baritula "sittoides"* flee from Bananaquits without (before) being attacked, and a female *D. baritula "sittoides"* retreat before *V. peregrina.* The usual dominance sequence in such habitats seems to be Bananaquits > *V. peregrina* > *D. baritula "sittoides."* The last is also attacked by *Zonotrichia capensis.* These unfriendly contacts might be described as normal rather than invariable. I have from time to time seen the three nectarivorous forms (and sparrows), all possible combinations of them, feeding close together without detectable hostility, but such peaceable behavior is somewhat exceptional.

The roles of *Colibri coruscans* at lower altitudes of the region are ambivalent and anomalous in a slightly different way. Individuals of the species fight among themselves but do not usually attack other species in and around the city. There is no doubt that individuals of *coruscans* are less irritated, more intimidated, and/or more successfully avoided by other species in the whole of the region of the Sierra de Mérida than in some other regions, such as the eastern cordillera of Colombia (see below). There is even some evidence that *coruscans* of Mérida, unlike its siblings and cousins of the higher altitudes of the same region, is partly incorporated into the local cluster of diglossas or diglossa-like birds. I saw several apparent examples of mutual avoidance and reciprocal inhibition of song between *coruscans* and Bananaquits in large gardens.

It might be mentioned, in passing, that the mixed but largely unfriendly interspecific reactions of the Bananaquits of Mérida are quite similar to those of other populations of the species in very different social contexts in distant regions, such as the lowlands of central Panama (see Moynihan, 1962c). Some aspects of the interspecific behavior of *Coereba* are both less conspicuously stylized and unbalanced, and more nearly uniform over vast distances, than those of many other nectarivorous birds. There may be some causal relationship involved.

The longest and most complex series of interspecific reactions seen in the region of the Sierra de Mérida occurred just outside Chorros de Milla. A large *Erythrina* tree there was in full flower in April of 1965. It was rather isolated, surrounded by pastures with scattered hedges and small patches of second-growth scrub, at the base of some fairly substantial foothills (perhaps 700–1,000 m above the floor of the valley in which the city is located). The flowers of the *Erythrina* were attractive to many birds. In the course of intermittent observations over a few days, I saw them visited by several Bananaquits, *D. baritula "sittoides"* of both sexes, at least two presumed *V. peregrina*, two or more *D. carbonaria gloriosa* (the form is not absolutely unadventurous or intolerant of unusual conditions), and one female *D. albilatera*. There also was *C. coruscans* in the tree, but I was not able to determine if it was feeding at the flowers or not. All these birds met one another from time to time. I saw close approaches without fighting between Bananaquits and *C. coruscans*, between the female *D. albilatera* and a *C. coruscans*, between a female *D. baritula "sittoides"* and a *D. carbonaria gloriosa* and between a pair of *D. baritula "sittoides"* and the female *D. albilatera*. I also saw a *D. carbonaria gloriosa* attack a female *D. baritula "sittoides"* repeatedly, a Bananaquit chase a male *D. baritula "sittoides,"* a pair of *D. baritula "sittoides"* chase a juvenile Bananaquit, a female *D. baritula "sittoides"* supplant the female *D. albilatera*, and a female *D. baritula "sittoides,"* perhaps the same individual, supplant an adult Bananaquit repeatedly. The female *D. baritula "sittoides"* finally supplanted a female American Redstart, *Setophaga ruticilla* (another "belated" migrant), on several occasions. Some of these incidents demonstrate that the usual dominance hierarchy among species is by no means rigid and can be subject to reversals.

Doubtless *D. carbonaria gloriosa* and the female *D. albilatera* were strays from higher altitudes. They illustrate the opportunism of many nectarivorous birds (Moynihan, 1968b). They cannot have been attracted directly; nectar as such is not visible at a distance. They may have been stimulated indirectly by the sight of the flowers, or even more indirectly by the activities of other birds at the flowers. It was noticeable that one or more of *D. c. gloriosa* usually visited the *Erythrina* immediately after *D. baritula "sittoides"* had arrived, and that *C. coruscans* was more likely to visit the tree when diglossas were present than when they were absent. There may be some personal attraction among the birds themselves, in spite of the risk for *D.*

c. gloriosa of becoming embroiled in disputes.

Other aspects of the behavior of the birds in this *Erythrina* revealed an ecological distinction. Two species, the Bananaquit and the presumed *V. peregrina*, preferred fresh, recently opened, flowers, while the diglossas *D. c. gloriosa* and *D. baritula* preferred riper or almost fading flowers, flowers presumably already visited by others. This sort of difference may be common in many areas and habitats, but it is seldom so visible to an observer.

There are barriers between members of the diglossa cluster of the Sierra de Mérida, but they are incomplete. It is suggested that the barriers seem to be even less effective at lower altitudes than at higher altitudes in the region. The lower habitats have been more greatly altered by man than have the higher ones, and are continuing to be transformed at a greater rate. They can be considered to be "newer" in an evolutionary sense. It would not be surprising if the social arrangements of their inhabitants were still somewhat provisional.

Sierra Nevada de Santa Marta

Forms of diglossas seen: *D. carbonaria nocticolor* and *D. albilatera* (*D. cyanea* may also occur, see below). Other members of the cluster are: *Myioborus flavivertex* and the hummingbird *Metallura tyrianthina*. Other probably relevant species are: *Myioborus miniatus, Atlapetes melanocephalus, Colibri coruscans*, and *C. thalassinus*.

The Sierra Nevada de Santa Marta is a high and isolated massif with a peculiar and perhaps not very rich fauna, including some distinctive endemics. The following account is both tentative and parenthetical to the main narrative. I visited the region only briefly and was not able to cover many sites or habitats. My observations were made in the vicinity of the field camp of the *Corporación del Valle del Magdalena* near San Lorenzo, around 2,300–2,500 m. Part of the area is cleared and consists of grasses, ferns, low scrubs, and only a few small trees. The rest, on very steep slopes, is lush and dense tall forest. The whole aspect is very humid. Most of the diglossas, hummingbirds, and many other birds were breeding or coming into reproductive condition, during the time of my visit (mid-August).

The most abundant species of diglossa is *albilatera*. I saw it most frequently in bushes and tangles at the edge of the forest, but it also ranges inside the forest, up in trees, and out in more open scrub. The local population seems to have a wider range of habitat preferences or tolerances than most other populations of the species elsewhere. Perhaps in correlation, the other bush diglossa of the region, *D. c. nocticolor*, is comparatively restricted. I saw only a few individuals in a few patches of semiopen scrub, mostly apart from tree cover. It was my impression that *D. c. nocticolor* is even less successful than *D. c. gloriosa*, which itself is less nearly ubiquitous, perhaps less adaptable, than *D. c. aterrima* or most of the other southern populations of the *D. carbonaria* group.

Although there is some habitat segregation between *D. albilatera* and *D.*

c. nocticolor in Santa Marta, it is only partial. Territories of the two forms may overlap completely. When overlaps occur, the individuals usually show mutual avoidance and reciprocal inhibition of song. I did, however, see several attacks by *D. c. nocticolor* upon male and female *D. albilatera*. Individuals of the two species may also come together without fighting when "escorting" mixed flocks (see below).

I heard some songs which sounded like those of *D. cyanea* in the forest on Santa Marta. The species is supposed to be absent from the region (de Schauensee, 1964), but the habitat looks suitable and it is conceivable that a small population exists or that strays arrive and survive for some time.

The whitestart *Myioborus flavivertex* is abundant on Santa Marta. It occurs in both forest and scrub. Its territories overlap those of both *D. albilatera* and *D. c. nocticolor*. There is very good, very nearly perfect, reciprocal inhibition of song between *M. flavivertex* and *D. albilatera*. The two species were heard to alternate phrases for many minutes on end without a single mistake. There also is good inhibition of song between *M. flavivertex* and *D. c. nocticolor*. There may be reciprocal avoidance of approaches between *M. flavivertex* and both diglossas. Another whitestart, widespread *M. miniatus*, was rare at the sites I visited on Santa Marta. It appeared to have avoidance and inhibition interactions with the diglossas and *M. flavivertex*. The local brush-finch *Atlapetes melanocephalus* was found almost everywhere in forest and scrub. There appeared to be a slight and imperfect tendency for *D. albilatera* to refrain from singing when the finches were most vocal.

As in most extremely humid areas, hummingbirds are particular conspicuous at Santa Marta. One of the common species is *Metallura tyrianthina*. At the time of my visit, the territories of this species completely overlapped those of *D. albilatera* and were at least adjacent to those of *D. c. nocticolor*. I did not have time or opportunity to investigate possible relations with *D. c. nocticolor*, but there was an obvious accommodation between these hummingbirds and *D. albilatera*. They fed on many of the same flowers. *M. tyrianthina* was seen to use incisions made by *D. albilatera* in bright orange tubular flowers. The two species seldom came into contact with one another. There may have been some slight inhibition of song between them. The usual avoidance might be due to fear on the part of *D. albilatera*. Once I saw a *M. tyrianthina* swoop repeatedly at a male *D. albilatera*. The social and ecological relations between *D. albilatera* and *M. tyrianthina* here may be much the same as the corresponding relations between *D. albilatera* and some other hummingbirds at La Palma in the southern part of the western cordillera of Colombia.

Colibri coruscans and the similar-looking *C. thalassinus* were both common on Santa Marta. They also were somewhat puzzling. *C. thalassinus* may be concentrated at lower altitudes than *coruscans* in some other parts of the Andes, at least at some times. When I worked near San Lorenzo both species perched frequently in trees around 2,300 m. *C. thalassinus* tended to pick areas of a few trees over low vegetation, grass, and ferns. *C. coruscans* preferred areas of lusher vegetation but also extended into *thalassinus*-type habitats. Certainly the overlaps of specific ranges and tolerances can be wide in this region. Significantly enough, however, the territories of the two species were mutually exclusive. Presumably this separation was initiated and maintained by hostility, but I did not see or identify fights between the two hummingbirds during my brief observations. I did see *C. coruscans* attack a male of *D. albilatera*, and a *D. c. nocticolor* attack a *C. thalassinus* repeatedly. (Individuals of *D. c. nocticolor* tend to be very aggressive. This is shown in their intra- as well as interspecific behavior.)

Eastern Cordillera of Colombia

Forms of diglossas seen: *D. cyanea*, *D. coerulescens*, *D. carbonaria humeralis*, *D. l. lafresnayii*, *D. albilatera*, and *D. baritula "sittoides."* Other probably or possibly relevant species are: *Conirostrum rufum*, *Myioborus ornatus*, *M. miniatus*, *Atlapetes pallidinucha*, *A. schistaceus*, *Colibri coruscans*, *Coeligena torquata*, *Lesbia nuna*, *Pterophanes cyanoptera*, and *Eriocnemis cupreoventris*. Other species of interest are: *Vermivora peregrina*, *Zonotrichia capensis*, *Spinus spinescens*.

The eastern cordillera of Colombia is large and long as well as high, but my observations were limited to the central part of the region, in the public parks and gardens of the National University in Bogotá at about 2,730–2,750 m, on the slopes of Cerro Guadalupe above the city from 2,700–3,000 m, on the road to Guasca about 26 km to the northwest of Bogotá at ca. 2,625 m, at the border of the páramo above Guasca (approximately 50 km from Bogotá along the road to Guachete) at ca. 2,900–3,000 m, on the road to the Lagunas de Chisacal, northeast of Bogotá, at a place called Santa Rosa at 3,150 m, and southwest along the highway to Agua Bonita and near La Aguadita at ca. 2,600–2,700 m. From the species lists available, all these areas would appear to be typical of the cordillera under present conditions.

Much of the region has a dense human population. Most areas are conventional mixtures of degraded forest and scrub, second-growth, hedges, gardens, etc. Only the alpine scrub just below the páramo of Guasca appeared to be almost natural during my earlier visits, and even this was being burned in April of 1965. The parks and gardens of Bogotá and elsewhere have the usual exotics.

Forms of diglossas and conebills seen near the páramo of Guasca and on Guadalupe included *D. cyanea*, *D. coerulescens*, *D. carbonaria humeralis*, *D. l. lafresnayii*, and *C. rufum*. de Schauensee (1966) says that *D. albilatera* also occurs near the same páramo. The corresponding forms seen in Bogotá were *D. carbonaria humeralis*, *D. baritula "sittoides,"* and *D. albilatera*. Around Agua Bonita and adjacent sites, the fauna included at least *D. cyanea*, *D. coerulescens*, *D. carbonaria humeralis*, *D. baritula "sittoides,"* and *D. albilatera* (also *Coereba flaveola* near La Aguadita). de Schauensee claims that *D. l. lafresnayii* may occur as low as 2,000 m in this region, but I saw it only at higher altitudes. I noted *D. carbonaria humeralis*, *D. l. lafresnayii*, and *C. rufum* on the road to Chisacal. A. Olivares (pers. comm.) found both *D. albilatera* and *D. baritula* "*sittoides*" at the same or nearby areas.

These observations and records indicate that the overlaps of *specific* ranges and habitats are greater, more extensive or frequent, in the eastern cordillera of Colombia than in the southern part of the western cordillera, the Sierra de Mérida, or the Quito region.

In other respects, however, the relations among the forms of the local diglossa cluster and rivals and associates are very different from those of the same or equivalent species in either the southern part of the western cordillera or central Ecuador. Both specialized avoidance and inhibition seem to be minimal, i.e., as slight as possible, in the eastern cordillera. They are even less evident or effective here than in the Sierra de Mérida.

The peculiarities of the region are best illustrated by *D. carbonaria humeralis*. The bird is almost ubiquitous at moderate to high altitudes in the region; it is obviously more successful than *D. c. nocticolor* or *D. c. gloriosa*, and more like *D. c. aterrima* in apparent adaptability. (Of course, the wide distribution of scrubby and semiopen vegetation in the region would be expected to favor any representative of *D. carbonaria*). Where *D. carbonaria humeralis* and *D. l. lafresnayii* occur in the same areas, they can react to one another in any one or all of several different ways. There may be some avoidance and/or inhibition. Or individuals of the two forms may simply ignore one another, approach or keep apart, or sing or refrain from singing simultaneously, apparently at random. Or they may tend to treat one another as if they were all members of the same species. Their territories may be exclusive, if adjacent or arranged in a mosaic pattern, without spatial overlaps. Their songs may also overlap in time. The sound of one species singing sometimes stimulates the other to sing before the first has finished. This can work both ways, *D. carbonaria humeralis* triggering *D. l. lafresnayii* and vice versa. There are many overt fights between the two forms. Most interspecific fights are won by *D. l. lafresnayii*. *D. carbonaria humeralis* in the end usually retreats before *D. l. lafresnayii*. Of course, *D. l. lafresnayii* is much the larger. But there also are suggestions that *D. carbonaria humeralis* is relatively more aggressive, gram per gram. Its retreats tend to be brief and slight. It may initiate many of the disputes, directly or indirectly, and I saw one reversal of the usual sequence, when a *D. carbonaria humeralis* defeated a *D. l. lafresnayii*.

The frequency of open hostility and interference between the two forms varies with time and place. Thus, for instance, disputes were much more common in April 1965 than in August of the same year, probably because more birds were crowded around special food sources, flowering eucalypts, during the earlier month than during the later one (see below).

Not entirely by chance, more birds of the cluster were in full breeding condition during August than during April. It seems to be a general rule among diglossas that face-to-face interspecific contacts, if they occur at all, tend to be rarer during the breeding season(s) than during the nonbreeding season(s), when and if the reproductive cycles of the different species coincide.

The lack of coincidence may help to explain the peculiar behavior of the *D. cyanea* near Nono in January 1964 mentioned above. The general correlation is only noteworthy in the case of *D. carbonaria humeralis* and *D. l. lafresnayii* because the two forms are virtually identical in plumage, and both show increased *intra*specific hostility when breeding. The fact that the two species do not vent this increased hostility on one another, do not fight with one another more frequently during the breeding season(s) than at other times, is good evidence for the existence of real social barriers, however imperfect, between them. (There are no records of hybrids. They might be difficult to detect in collections. But the songs of the two forms are different, and I did not hear any vocalizations that were certainly intermediate. This, in turn, is evidence that the variability of some other kinds of social behavior is not due to introgression.)

Relations between *D. carbonaria humeralis* and *D. l. lafresnayii* and the other diglossas of the eastern cordillera, and among the latter, are also somewhat uneasy. There is wide overlapping of feeding habits and of territories, apart from the *D. carbonaria humeralis-D. l. lafresnayii* rivalry, with many lapses of social caution. *D. carbonaria humeralis* tend to be careless or aggressive in all relations. I saw repeated attacks by many *D. carbonaria humeralis* upon *D. cyanea*, temporary associations without fighting between the same two forms, several cases above Guasca of *D. carbonaria humeralis* following *D. coerulescens*, a few attacks by *D. carbonaria humeralis* upon *D. coerulescens* on Guadalupe, repeated attacks by *D. carbonaria humeralis* upon both male and female *D. baritula* "*sittoides*" in Bogotá, approaches and contacts without fighting between the same two forms, at least one attack by *D. carbonaria humeralis* upon a female *D. albilatera* in the same area, and attacks by *D. carbonaria humeralis* upon hummingbirds, e.g., *Colibri coruscans, Eriocnemis* sp., and a miscellany of birds of other groups, both resident and migrant warblers (including *Basileuterus nigrocristatus* and probably *Vermivora peregrina*), various small tanagers, and some finches (*Zonotrichia capensis* and *Spinus spinescens*). The last attacks seemed to be expressions of general aggressiveness rather than specific dislikes. Local *Zonotrichia* and *Spinus* paid only occasional attention to flowers. (*D. carbonaria humeralis* may or may not be more aggressive than *D. carbonaria nocticolor* on the average. The areas in which I observed *humeralis* provided more opportunities for interspecific encounters than did the area visited at Santa Marta where *nocticolor* is found.)

The social carelessness of the diglossas of the eastern cordillera is equally manifest in their singing behavior. Occasional overlaps of songs occur among all possible combinations of species. They are comparatively common in the region, apparently more common here than in all or most other regions, although still definitely not the general rule. Perhaps surprisingly, I heard many overlaps of songs between *D. l. lafresnayii* and blue diglossas, both *D. cyanea* and *D. coerulescens*. The blue birds seemed to be stimulated by the *D. l. lafresnayii* more often than the reverse. On the other hand, *D. cyanea* and *D. coerulescens* usually were careful *not* to sing simultaneously with one another. The relations between these two species are the best example of social segregation in the region.

It should be mentioned that individuals of *D. coerulescens* seem to be more abundant and widely distributed in the eastern cordillera than in other regions. They were seen to eat many small fruits at Guasca and other sites, while local *D. cyanea* appeared to be almost confined to nectar and small arthropods (note the contrast with the Sierra de Mérida). Perhaps *D. coerulescens* of the eastern cordillera has occupied part of the niche usually preempted by or reserved for *D. cyanea* elsewhere. The ecological differences between the two species seem to be less clear in the eastern cordillera than in all or most other regions (note the contrast with the southern part of the western cordillera of Colombia).

A further peculiarity of the diglossas of the Bogotá region is their tendency to form groups in certain circumstances. In April 1965 I found concentrations of diglossas and some hummingbirds in two areas, viz., in the gardens of the university, especially around *Kniphophora* and red and yellow *Abutilon*, and on Guadalupe in flowering eucalypts (probably *Eucalyptus globulus*). In the university gardens the common forms were *D. carbonaria humeralis*, *D. baritula* "*sittoides*," and *Colibri coruscans*. The concentration in the eucalypts included *D. cyanea* and *D. coerulescens* (not simultaneously), *D. carbonaria humeralis, D. l. lafresnayii*, *Lesbia nuna*, and *Eriocnemis* sp(p). In early September 1974 I found another concentration in other flowering eucalypts on Guadalupe, perhaps one kilometer from the site of the first group (no longer present as such). The new concentration included relatively more blue birds, probably all *D. cyanea,* but was otherwise similar in species composition to the earlier assemblages on the mountain.

The groups were reminiscent of the concentration in the *Erythrina* in Chorros de Milla, but larger and more tightly packed. There were often some 10–15 individuals of *D. carbonaria humeralis* in a space of approximately 7 × 10 × 7 m in the eucalypts—the nearest approximations to real flocks of diglossas that I have ever seen.

Relations between honeycreepers and hummingbirds in the eastern cordillera are combinations of frequent hostility with some regular "parasitism." This, in itself, is quite usual and conventional. It does not mean that every species plays the same role(s) in the eastern cordillera as elsewhere. *Colibri coruscans*, for instance, is bolder or less detached in and around Bogotá than in the Sierra de Mérida. There were many disputes between *D. carbonaria humeralis* and *C. coruscans* in the gardens of the university. Sometimes a *C. coruscans* flew at and tried to attack a *D. carbonaria humeralis*. More often a *D. carbonaria humeralis* dashed at a *C. coruscans*. Neither kind of attack was often pressed home. The aggressor usually swerved or braked at the last moment. The two species would seem to have almost equal rank in the interspecific hierarchy of the region. *C. coruscans*, like *D. carbonaria humeralis* (see above), attacked and supplanted both male and female *D.*

baritula "*sittoides*." It would appear that *D. baritula* "*sittoides*" is subordinate here, as it is in the Sierra de Mérida and other regions. The Bogotá birds are, however, practically undiscourageable. They keep coming back. Their persistence must be facilitated by one habit. All diglossas can penetrate inside tangles or thickets of interlocked branches and twigs. Most hummingbirds, and certainly *C. coruscans*, tend to remain hovering on the outside. Thus *D. baritula* "*sittoides*" can take refuge from *C. coruscans* by bolting inside where the hummingbirds cannot or will not follow. (Specific differences in behavior do not disappear in flocks or concentrations. Even in the eucalypts of Guadalupe, the blue diglossas tended to remain in the tops of the trees while *D. carbonaria humeralis* and *D. l. lafresnayii* also ranged through lower branches.) *C. coruscans* of the university gardens visited holes cut by diglossas and apparently extracted nectar from them. In other areas I saw other hostile encounters, e.g., attacks by *Eriocnemis cupreoventris* upon *D. carbonaria humeralis* and *D. l. lafresnayii* on Guadalupe (apart from the flowering eucalypts), an attack by a *D. l. lafresnayii* upon a *Pterophanes cyanoptera* above Guasca, and an attack by a *Lesbia nuna* upon a *D. l. lafresnayii* at Santa Rosa. The *Eriocnemis*, at least, also used the holes of diglossas.

I did not notice any inhibition of song between diglossas and hummingbirds in this region.

The conebill *C. rufum* is not uncommon in the eastern cordillera. It seems to be intermediate in some aspects of social behavior between *C. cinereum* on one hand and *C. sitticolor* and *C. albifrons* "*atrocyaneum*" and *C. a. albifrons* on the other hand. It occurs both by itself and in mixed flocks of tanagers, finches, etc. The individuals that I saw were gleaning insects from leaves, but the species presumably is also adapted or pre-adapted to taking nectar. Whatever the competition, the local diglossas and hummingbirds usually ignore it. They may be more concerned with whitestarts and *Atlapetes* spp. The whitestarts are not particularly abundant in the region, and brushfinches are difficult to see, but I thought that there was the usual amount and types of variation in behavior among them and between them and diglossas, and perhaps conebills.

Central Cordillera of Colombia

The central cordillera is relatively large. It is comparable to the eastern cordillera in extent but more closely connected to, and essentially continuous with, the main mass of the Andes in the Nariño region of the south of Colombia and in Ecuador (see map, p. 8). In a sense it is only a prolongation of the central Andes as a whole. It does, however, have other relations. Its southern end is not far from the eastern cordillera of Colombia, and its northern end approaches the high peaks of the western cordillera. These relations are reflected in different ways in its biota(s).

I worked in several parts of the central cordillera. Most attention was paid to the birds of the volcano of Puracé and its surrounding foothills and ridges in the southern part of the cordillera to the east of Popayán. I worked on both slopes of the volcano along and around the road from Popayán to Neiva, on the western slopes from just above the town of Puracé, and in the nearby finca of "Canaan," ca. 2,700–2,800 m. I also worked at approximately 40–42 km from Popayán, up to the pass at the edge of páramo at ca. 3,100–3,400 m, at approximately 54–55 km along the road, and down the eastern slopes, in the district of Moscopán, almost as far as the village of Tijeras at ca. 2,725 m and 80 km from Papayán. This transect passed through many habitats. There were gardens and hedges in Canaan and elsewhere just above Puracé. There was beautiful and rich "alpine" scrub at higher altitudes. The natural vegetation of Moscopán and near Tijeras would be lush "upper subtropical" forest. Unfortunately, much of the forest by the road had been cut before my observations, and so recently that there was little second-growth edge vegetation except for patches of thorny and almost impenetrable bamboo thicket. (This is the classic environment of the Spectacled Bear, *Tremarctos*, and the Mountain Tapir, *Tapirus pinchaque.*) The forms of diglossas on Puracé include *D. cyanea, D. coerulescens, D. carbonaria aterrima, D. l. lafresnayii*, and *D. albilatera*. Other species of the cluster are *Conirostrum cinereum*, the whitestart *Myioborus ornatus*, the usual brush-finches *Atlapetes schistaceus* and *A. rufinucha*, and even little-known *A. leucopis.* Other relevant species include the hummingbirds *Colibri coruscans, Aglaeactis cupripennis, Ramphomicron microrhynchum*, and *Eriocnemis mosquera.*

These diglossas and conebills are very similar to or identical with the forms of central Ecuador in appearance. The resemblance between the two regions extends to relative population sizes. As in Ecuador, only four forms are abundant on Puracé: *D. cyanea, D. carbonaria aterrima, D. l. lafresnayii,* and *C. cinereum.* I saw only one or two *D. coerulescens* in low and dense bush, and a small population of *D. albilatera* on the eastern, wetter slopes of Puracé.) The ecological and habitat preferences and ranges of the common forms also seem to be much the same on Puracé as around Quito. It is remarkable, therefore, that *some of the behavior patterns of the Puracé birds are quite different from those of their close relatives in central Ecuador; they are more like those of the birds of the eastern cordillera of Colombia.* Their interspecific reactions are both varied and messy. Separation, segregation, and inhibition are incomplete or intermittent in most cases. Face-to-face encounters, with or without open hostility, and overlaps of songs are comparatively common. The interspecific relations of the Puracé birds are, in fact, so reminiscent of the eastern cordillera that it would be superfluous to describe them at length. It is only necessary to note a few of the most significant features, complications, and exceptions.

D. carbonaria aterrima is less similar to *D. l. lafresnayii* in color pattern than is *D. carbonaria humeralis.* Possibly, therefore, the territories of *D. carbonaria aterrima* and *D. l. lafresnayii* on Puracé are less often mutually exclusive than are the territories of *D. carbonaria humeralis* and *D. l. lafresnayii* in the eastern cordillera, i.e., there is less tendency for the two species to treat one another as members of the same species. In this respect, *D.*

carbonaria aterrima and *D. l. lafresnayii* of Puracé recall the corresponding birds of Ecuador. But there is still a great deal of hostility and other interference between them. Their reactions to one another are very different from the careful segregation in Ecuador, but similar to the reactions among most other diglossas in the same or other "intermediate" regions of the northern Andes. As usual when there are hostile encounters between *D. carbonaria* and *D. lafresnayii*, it is the latter that is dominant. *C. cinereum* was not seen to fight with or be attacked by diglossas or hummingbirds on Puracé. This may be the one full member species of the local cluster that is generally protected by an Ecuadorean-type system of social segregation. My observations would suggest that there may also be segregation and inhibition between *D. coerulescens* and *D. cyanea* on Puracé, although certainly not between either and most other species in the same areas.

The hummingbirds of Puracé provide examples of almost all kinds of possible interactions with diglossas and among themselves.

Aglaeactis cupripennis is one of the most abundant and conspicuous species. It is definitely nomadic or migratory. It was common a few hundred meters below the edge of the páramo in May 1965, but concentrated at lower altitudes, especially at Canaan, in August of the same year and in September 1974. It is exceedingly aggressive at all times wherever it occurs in the region. The species initiates or becomes involved in interspecific hostilities very frequently on Puracé, relatively much more frequently than in central Ecuador. I saw many swoops and attacks by *A. cupripennis* upon a great variety of other species on Puracé, as for example upon many individuals of *D. l. lafresnayii*, *D. carbonaria aterrima*, and *D. cyanea*, and also on small hummingbirds of the species *Ramphomicron microrhynchum*, and even on such different birds as the large thrush *Turdus fuscater*. The encounters with diglossas were not all of a piece. Attacks upon *D. l. lafresnayii*, common in terms of actual numbers, were relatively much rarer than attacks upon either *D. cyanea* or *D. carbonaria aterrima*. *D. l. lafresnayii* is large and presumably imposing enough to be slightly intimidating. In any case, *D. l. lafresnayii* tended to ignore the attacks of *A. cupripennis*. Attacked *D. cyanea*, on the other hand, usually retreated or fled more or less promptly. *D. carbonaria aterrima* appeared to be less imposing than *D. l. lafresnayii* but was much more overtly pugnacious. It sometimes counterattacked. I also saw some attacks by *D. carbonaria aterrima* upon *A. cupripennis*. It would seem that the relations between these birds on Puracé are much the same as those between *D. carbonaria humeralis* and *Colibri coruscans* in the gardens of the university in Bogotá.

A. cupripennis, diglossas, and other nectarivorous birds often feed on the same flowers on Puracé as elsewhere. It may be assumed that their interspecific hostility is somehow related to the competition among them. At least in the case of *A. cupripennis*, however, the correlation is more general or remote than precise or immedate. It is not dependent upon particular feeding habits or preferences at any given instant of time. *A. cupripennis* made many attacks upon diglossas at Canaan when they all, hummingbirds and honeycreepers alike, were feeding on flowers in the garden or the adjacent scrub (see details below). The same species made a comparable number of attacks at higher altitudes in May 1965 when the diglossas were feeding most frequently on some dark red cup-shaped melastomaceous flowers that *Aglaeactis* did not like very much. (Many species of montaine melastomes are favorites of honeycreepers but less attractive to hummingbirds.) More surprisingly, *A. cupripennis* usually ignored individuals of *Eriocnemis mosquera* everywhere on Puracé, even though the latter are often conspicuous and visit some of the same flowers (not usually melastomes or in gardens). The situation is further complicated by other factors. I did not see *Aglaeactis* use diglossa holes in flowers on Puracé. *E. mosquera*, however, certainly does so on occasion, and probably quite regularly. It also likes the same dark red melastomes as the diglossas. But it manages to tap these resources with a minimum of trouble. I did not see any attacks by either *Aglaeactis cupripennis* or diglossas on *E. mosquera*. Considering the aggressive, irritable temperaments of both *A. cupripennis* and *D. carbonaria aterrima*, this must, I think, mean that *E. mosquera* is careful to avoid contacts with some or all competitors. This is in contrast to other species of *Eriocnemis* in such regions as the eastern cordillera of Colombia.

Ramphomicron microrhynchum, another hummingbird, was also common at Canaan during my observations. Several individuals of both sexes ranged widely in and around the garden, through the territories of all the other kinds of nectarivorous birds. They were frequently attacked by *Aglaeactis* and occasionally supplanted by *D. cyanea* and *D. carbonaria aterrima*. They also appeared to have more positive links to the latter. Both *D. carbonaria aterrima* and *Ramphomicron* often fed in the same bushes and tended to do so simultaneously. They were together more often than would have been expected by chance alone. I could not tell which was attracted to which. The association may have been advantageous to *Ramphomicron* for several reasons. It increased the chances of attack by *D. carbonaria aterrima* but decreased the danger from the even more aggressive *Aglaeactis*. Whenever *A. cupripennis* encountered *D. carbonaria aterrima* and *Ramphomicron* together, it was likely to ignore the latter and attack the former instead. *D. carbonaria aterrima* seemed to function as a decoy or buffer for *Ramphomicron* in these circumstances. As a possible added benefit, the diglossas also attacked, perhaps preferentially, other smaller and unidentified hummingbirds that may have been further competitors of *Ramphomicron*. In this case they also functioned as inadvertent allies of their victims in a very different way.

Colibri coruscans occurs in many habitats on Puracé. I saw fights between *C. coruscans* and *Aglaeactis cupripennis*, but almost no hostile encounters between *C. coruscans* and diglossas. *C. coruscans* may be as mild in this region as it is in the Sierra de Mérida. Possibly it is partly integrated with the cluster as are the birds of Chorros de Milla. I noted some sporadic or intermittent traces of avoidance and inhibition between *C. coruscans* and three of the local diglossas, viz., *D. cyanea*, *D. carbonaria aterrima*, and

D. l. lafresnayii, as well as the common whitestart, *M. ornatus*. (Doubtless Andean hummingbirds show as much geographic variation in behavior as do diglossas, tanagers, and many other birds.)

Canaan is an area that reveals and emphasizes ecological differences. The largely native scrub next to the garden is full of flowers, mostly small and yellow, cream, or white. Many of these are visited by all the local nectarivores, *D. carbonaria aterrima, D. cyanea, C. cinereum, Aglaeactis cupripennis, Ramphomicron*, other small hummingbirds, and also a few *D. l. lafresnayii* (probably strays from higher altitudes). The garden itself includes many geraniums, chrysanthemums, and daisies, and literally thousands of *Kniphophora*. The geraniums and composits are ignored by all the birds. The *Kniphophora* were tapped repeatedly, almost constantly, by *D. l. lafresnayii, D. carbonaria aterrima*, and *Aglaeactis*, but never by any of the others. The number of individuals was greater in the *Kniphophora* beds than in the scrub, even though the number of species was smaller. I did not see any *Colibri coruscans* in either the garden or its immediate vicinity. All nectarivorous birds may be more or less opportunistic, but they do not always adapt to every artificial environment equally easily or frequently.

There are a few *D. baritula* "*sittoides*" in gardens, hedges, and second-growth along streams in and around the city of Popayán at ca. 1,730 m. They share these habitats with *Coereba, Colibri coruscans* (demonstrating flexibility here), and another rather large hummingbird, *Anthracothorax nigricollis*, but the four species are so rare in the area that they seem to have few opportunities to interact. They certainly did not interact in any interesting ways while I watched them.

I did not see any *D. baritula* "*sittoides*" on Puracé, not even in gardens. The central cordillera may be another region in which these birds are discouraged by *D. carbonaria*. There is some reason to believe that the discouragement might be severe. I never found *D. baritula* "*sittoides*" in the same areas as *D. carbonaria aterrima* anywhere in the Andes. *D. carbonaria aterrima* may be more effective as a competitor of *D. baritula* "*sittoides*" than all or most of the other subspecies of *D. carbonaria*.

Perhaps significantly, *D. coerulescens* is also absent or very rare in areas where *D. carbonaria* is present. (The only place where *D. coerulescens* was seen on Puracé was Moscopán, and this is almost outside the usual range of *D. carbonaria aterrima*.) Given their different preferences, the two forms are not likely to be competing seriously with one another directly. It is conceivable, however, that there are indirect ricochet effects. Some third species, perhaps *D. cyanea*, may be affected by *D. carbonaria aterrima* in such a way as to make it (even) more dangerous to *D. coerulescens* than it would be in other circumstances. Thus, *D. carbonaria aterrima* could be the impulse for a whole series of shifts of adaptive zones.

The brush-finches of Puracé are conventional in behavior but local *Myioborus ornatus* may be a slightly unusual. It appears to be as closely linked to the local diglossas as most of the latter are to one another. I saw it attack and chase both *D. l. lafresnayii* and *D. cyanea*. Yet it tends to refrain from singing at the same time as the diglossas, even *D. carbonaria aterrima*, and also (by extension?) at the same time as *Colibri coruscans*. Its singing control is surprisingly good.

The northern part of the central cordillera has its own distinctions. I made brief visits, a few days at a time, to several sites in the north near the city of Medellín, viz., Boquerón de Palmitas, the finca "La Montaña" near La García, the environs of the settlement or suburb of Santa Elena, Piedras Blancas, and the district of Belmira near El Llerbal. All these sites are between 2,400 and 2,550 m, thus they are moderately low. At the times of observations, La Montaña and Santa Elena were largely gardens, Belmira was varied, and Palmitas and Piedras Blancas were somewhat more nearly natural with more scrub. Large and mature trees were scarce everywhere. The area as a whole is either less humid or much more degraded than most of Puracé.

Forms of diglossas seen in the north: *D. cyanea*, *D. coerulescens*, *D. carbonaria brunneiventris*, and *D. albilatera*. Other probably revelant species: *Myioborus ornatus*, *M. miniatus*, *Atlapetes rufinucha*, *A. schistaceus*, and *Colibri coruscans*. (*Conirostrum cinereum* seems to be lacking, and *D. lafresnayii* must be absent or very rare.)

This mix of honeycreepers is different, in terms of component species and subspecies, from that of the southern part of the same cordillera. As would be expected, the ecological relations among them are also different in some respects. *D. carbonaria brunneiventris*, for instance, is restricted around Medellín. It is apparently less successful than is *D. c. aterrima* of Puracé. It seems to be almost confined to patches of not very dense scrub and hedges and was seen only at Belmira. *D. coerulescens*, on the other hand, appeared to be relatively abundant at Santa Elena and Piedras Blancas, less rare than its relatives on Puracé although still far from common. The northern birds were concentrated in the thickest scrub and the few small trees available. (Santa Elena and Piedras Blancas are comparable to Moscopán in being at a relatively low altitude for the species.) The predominant forms of the northern sector of the central cordillera of Colombia are *D. cyanea* and *D. carbonaria aterrima*. This is reminiscent of some other regions of the northern Andes, such as the Sierra de Mérida.

As far as I know, there are no abrupt geographic or ecological barriers in the middle of the central cordillera that could explain the various differences between the birds at the two ends of the cordillera. Apparent gaps, such as may exist between *D. carbonaria brunneiventris* and *D. c. aterrima*, are often problematical (see Diamond, 1972, 1973, and 1975). There may be obscure agents, e.g., parasites or pathogens, at work (see Cornell, 1974, for some possibly similar cases). More important, immigration into the region seems to have come, and may be coming still, from opposite directions, i.e., from the northern extension of the main mass of the central Andes in Nariño (where the species and subspecies mix is the same as on Puracé) and from the northern part of the western cordillera of Colombia (where the mix is more reminiscent of the Medellín area). Human activities may also be significant. Any one or all of these factors, in combination with slight differences in selection pressures (and the pressures cannot be absolutely identical at the two ends of the chain), could be adequate to account for the incongruence observed.

What might not have been expected—but nevertheless is true—is that the social behavior patterns of the members of the diglossa cluster of the northern part of the central cordillera of Colombia are much the same as those of the members of the cluster in the southern part of the same cordillera, *even though* the members themselves are different and have somewhat different ecological preferences or tolerances. The northern birds have variable interspecific responses, with incomplete separation, segregation and inhibition, and considerable overt hostility, more or less like their counterparts on Puracé.

These anomalous differences and similarities are problematical, but they do serve to show that social behavior, within broad limits, is *not always directly dependent upon phylogenetic relationships or correlated with immediate aspects of ecology*. Some of the reasons why this should be so are considered on p. 86 et seq.

A further note may be added for reasons of comparison. *D. cyanea* and *D. carbonaria brunneiventris* of the northern part of the central cordillera are typical of their species in their choices of levels of vegetation. Whenever conditions permit, the blue birds visit trees more frequently, and tend to go and remain higher in them, than do the black and brown birds.

Northern End of the Western Cordillera of Colombia

My work in the region was brief and hurried with only a few days near Boquerón de Tello, ca. 2,000–2,350 m, in October 1962, and along the slopes of the valley of the Río Urrao up to the Páramo Frontino, ca. 2,700–3,200 m, in July 1965. Both areas are west of the town of Antioquia.

Frontino is the more significant and interesting of the two, with lush "upper subtropical" forest at lower altitudes and "alpine" scrub higher at the border of the páramo itself (some or all of the scrub had been burned a few years before my observations, but it was regenerating or growing vigorously). The forms of diglossas seen included *D. cyanea, D. coerulescens, D. carbonaria brunneiventris, D. lafresnayii gloriosissima,* and *D. albilatera*. Other relevant species were *Myioborus ornatus, Atlapetes schistaceus, Colibri coruscans, Heliangelus exortis,* and *Coeligena torquata*.

Relations among members of the diglossa cluster in this region are most reminiscent of the southern part of the same cordillera. There are also some echoes of the central cordillera and a few features that are unique.

D. lafresnayii gloriosissima is relatively rare and apparently confined to scrub and edges of forest at the highest altitudes, only a few meters or tens of meters below the edge of the páramo. *D. carbonaria brunneiventris* is common and widely distributed from the edge of páramo down to the lowest altitudes at which observations were made. Its distribution completely overlaps that of the *D. lafresnayii gloriosissma*. In areas of overlap the two forms seem to have similar or identical habitat preferences. They certainly feed on many of the same kinds of flowers, including the same dark red melastomes as on Puracé. In these circumstances, it is not entirely surprising that their individual territories are mutually exclusive, especially as the two forms have similar plumage color patterns. (The exclusiveness and the degree of resemblance are comparable here and in the eastern cordillera of Colombia. Only the actual color patterns are different.) Possibly this territorial arrangement is initiated or maintained by hostile behavior. I did not, however, see any overt fighting between the two species while I was at Frontino. Nor did the songs of the two species overlap, except on very rare occasions or when individuals were very far apart (possibly not even in earshot of one another when and if the individuals were low in thick scrub). The songs of *D. lafresnayii gloriosissima* are, in fact, seldom obscured by any other member of the cluster. Aside from *D. carbonaria brunneiventris*, other diglossas are rare or absent in areas with *D. lafresnayii gloriosissima*. Both *Myioborus ornatus* and *Atlapetes schistaceus* are moderately abundant. The territories of both overlap those of *D. lafresnayii gloriosissima* but their songs usually do not. I heard no overlaps of songs between *D. lafresnayii gloriosissima* and the whitestarts, and only a few with brush-finches.

At Frontino, as in many other regions, *D. albilatera* seems to be confined to humid scrub at comparatively low altitudes, often under trees. Only one *D. coerulescens* was seen at Frontino, in dense but uncovered scrub at a moderate altitude. *D. cyanea* is more widely distributed but concentrated at the lower altitudes. There is some overlapping of territories among these forms and *D. carbonaria brunneiventris*, *Atlapetes schistaceus*, and *Myioborus ornatus*, and also partial reciprocal inhibition of songs among them and between them and the whitestarts and brush-finches.

Other aspects of the relations between local *D. cyanea* and *D. carbonaria brunneiventris* are peculiar. At the higher altitudes of Frontino, most individuals of *D. carbonaria brunneiventris* usually remain fairly low in scrub, like other representatives of *D. carbonaria* elsewhere. At somewhat lower altitudes they often go high into trees, up to at least 15 m above ground. In the same areas it is *D. cyanea* that tends to spend much or most of its time low in scrub. The two populations have, in these areas, *exchanged* the preferences for particular levels of vegetation that are characteristic of their species almost everywhere else. *D. carbonaria brunneiventris* being high and *D. cyanea* low, instead of the reverse as would have been expected. There are other and correlated reversals. In most parts of the Andes *D. cyanea* is more likely to associate with mixed flocks, and does so in a more friendly manner, than any other diglossas. At the lower altitudes of Frontino, by contrast, *D. carbonaria brunneiventris* seems to join and follow flocks more frequently than does *D. cyanea*. These features suggest that different kinds of diglossas are almost ''equipotential,'' and that almost any one of them can play the social and ecological roles of any other in appropriate circumstances. There is supporting evidence from Central America (p. 72). Doubtless exchanges (or ''cross-overs,'' to use the term of Cody, 1974) are due to factors that are more or less historical. The *D. cyanea–D. carbonaria* *brunneiventris* reversal in the northern part of the western cordillera is perhaps less likely to be a persistent result of some "accident" remote in time (such as the first order of appearance of the species in the region) than of more recent events. Antioquia (with Medellín) has been a center of particularly intensive human colonization (see, for instance, Parsons, 1949). Much of the vegetation has been cleared repeatedly. The birds of forest and scrub may have been decimated or exterminated again and again. Repeated drastic reductions of populations, with inevitably different effects upon different species, might be expected to permit or favor changes of niches and ranges. It is tempting to suggest that the anomalous distributions of some species and subspecies in the western cordillera and the northern part of the central cordillera are examples of this phenomenon. One can imagine a variety of scenarios for each particular case. Unfortunately, it is impossible to choose among them in the absence of evidence. In any case, the *D. cyanea–D. carbonaria brunneiventris* exchange has occurred in the parts of the humid cold zone that are most accessible to human exploitation.

The exchange illustrates a connection between habitat or microhabitat preference and some aspects of social behavior in an unusually clear, almost textbook, fashion.

The hummingbird *Heliangelus exortis* interacts with several diglossas at Frontino. I saw three or four individuals of the species attacked by *D. carbonaria brunneiventris,* and a single individual repeatedly attacked by a male *D. albilatera. Colibri coruscans* is widespread in the region but apparently does not pay much attention to the honeycreepers here, perhaps because most of the diglossas are not very common. I did see a male *Ramphomicron* retreat before a *C. coruscans. Coeligena torquata* also occurs. Neither *Ramphomicron* nor *Coeligena* seemed to react to the diglossas at Frontino. *Coeligena torquata* may be less aggressive here than in the southern part of the same cordillera.

The Boquerón de Tello area is rather poor scrub with a few trees. The relevant species seen in 1962 were *D. albilatera, D. baritula "sittoides,"* and the small peculiar finch or "grassquit" *Tiaris olivacea.* A single *D. cyanea* may have been heard but was not seen. The territories of the various forms were partly overlapping but their songs were seldom synchronous. The songs of local *D. baritula "sittoides"* are largely twittering, reminiscent of *D. carbonaria brunneiventris* and other forms of the *D. carbonaria* group. The songs of *D. albilatera* are trills or rattles, as in central Ecuador and elsewhere. The songs of this species seem to vary less, from region to region, than do those of some other diglossas and conebills. The songs of *Tiaris olivacea* of Boquerón de Tello are also trills or rattles, quite *D. albilatera*-like in sound. The species is widespread, and its songs do not seem to be any more variable than those of *D. albilatera*. It should adapt to the reciprocal inhibition of song system quite easily. Perhaps it would be incorporated into the system more frequently if it were not primarily a species of relatively low altitudes and open habitats. It can hardly come into significant contact with diglossas in most regions. Its association with diglossas at Boquerón de Tello reflects both the lowness of the area and the degradation of the local habitat.

Northern Peru West of the Marañón

Geographically, this sector of Peru is a solidly connected southern extension of the main central mass of the Andes that also includes the Quito region (see map, p. 8). My work was confined to the neighborhood of the town of Cutervo where there are gardens, hedges, and second-growth scrub in the immediate vicinity of the town, at ca. 2,600 m, and more natural-looking "alpine" vegetation at higher elevations, up to 3,100 m. Among the birds seen were *D. cyanea, D. carbonaria aterrima, C. cinereum, Aglaeactis cupripennis, Colibri coruscans,* and *Atlapetes rufinucha*. Most of them behaved in much the same ways as in similar environments near Quito.

The local representatives of *A. cupripennis* were not seen to attack diglossas, although they are aggressive toward some other birds that were members of mixed flocks. Thus, they may be more closely associated with the diglossa cluster than are their relatives in central Ecuador, and even more different from their relatives on Puracé, Colombia.

I did not encounter whitestarts anywhere in northern Peru. Both *Myioborus melanocephalus* and *M. miniatus* are supposed to occur in these regions (de Schauensee, 1966), but they must be rare and/or scattered.

Northern Peru East of the Marañón

I worked in and around the town of Chachapoyas. This is at essentially the same latitude as Cutervo, and only a few kilometers distant in a straight line. As would be expected the two areas have similar ranges of habitats at the same elevations. They are, however, separated from one another by the deep cleft of the valley of the upper Marañón River. The cool tropical part of the Chachapoyas region is much less broadly or directly connected to the main mass of the central Andes than is the equivalent life zone of the Cutervo area (see map, p. 8).

Forms of diglossas seen near Chachapoyas: *D. cyanea, D. coerulescens, D. carbonaria brunneiventris, D. lafresnayii unicincta,* and *D. baritula "sittoides."* Another member of the cluster: *C. cinereum.* Other relevant species: *Aglaeactis cupripennis, Colibri coruscans*, and a smaller hummingbird, *Leucippus taczanowskii.*

The particular habitats visited were hedges (some with many eucalypts) and patches of dense second-growth scrub within and on the outskirts of the town at ca. 2,180–2,440 m, and lusher, more varied, and apparently older scrub and forest on the nearby hill of Tinaja at ca. 2,400–2,800 m. Much of the region is reminiscent in appearance of the Medellín area and the northern part of the central cordillera of Colombia. It may be less than maximally humid and/or have been cleared repeatedly.

The common forms of the lower and more suburban habitats, in order of abundance, are *D. carbonaria brunneiventris, C. cinereum*, and *D. baritula* "*sittoides.*" The relations among them are rather stereotyped. Their ecological preferences are broadly overlapping. They use many of the same kinds of trees and shrubs. *D. carbonaria brunneiventris* and *D. baritula* "*sittoides,*" at least, sometimes feed on the same kinds of flowers. *C. cinereum* is more often arboreal than are either *D. carbonaria brunneiventris* or *D. baritula* "*sittoides.*" (Southern *C. cinereum* goes into trees slightly more frequently, and perhaps averages higher, than do northern populations.) In these circumstances it is interesting that territories of individuals of different species usually are more or less exclusive. With occasional exceptions they are distinct or overlap only at the edges, although they are often adjacent and intermingled in mosaic fashion. There also is good, if not perfect, reciprocal inhibition of songs among the three species at these lower sites. Some or all of their territorial exclusiveness may be maintained by hostility. I saw a male *D. baritula* "*sittoides*" retreat before a *D. carbonaria brunneiventris*.

There is a peculiar problem associated with the local *D. baritula* "*sittoides.*" In the northern Andes (as at Boquerón de Tello), the songs of males of this group are more or less twitterings. Minor or accessory rattle components are combined with the twitters in some places. I think that all the males of any given area of the northern Andes tend to utter similar songs. The situation is different near Chachapoyas. Here, some of the males utter pure trills while others utter long phrases of pure or nearly pure twitters. The difference appears to be constant. Males of the two types also tend to alternate their songs, to refrain from singing synchronously, just as if they were members of different species. Perhaps this area is a zone of secondary contact between two populations that have developed, or are developing, barriers to free interbreeding.

Hummingbirds are plentiful around Chachapoyas. Near the town individuals of *Leucippus taczanowskii* feed very frequently upon flowers of maguey, *Agave* sp. So do individuals of *D. baritula* "*sittoides.*" Sometimes the hummingbirds and diglossas seem to ignore one another. At other times, *Leucippus* attacks *D. baritula* "*sittoides.*" *Colibri coruscans* also occurs in the area. It does not often feed on *Agave*, but it is very aggressive toward *Leucippus*. It obviously attacks *Leucippus* more frequently than it does *D. baritula* "*sittoides.*" Thus *Leucippus* probably provides some relief as well as competition for *D. baritula* "*sittoides.*"

On Tinaja both *C. cinereum* and *D. baritula* "*sittoides*" seem to be very rare or absent (I did not see either of them), but *D. carbonaria brunneiventris* is common and there are small populations of *D. cyanea*, *D. coerulescens*, and *D. lafresnayii unicincta*. *D. carbonaria brunneiventris* was found everywhere on the mountain, from top to bottom. *D. lafresnayii unicincta* was found only around 2,600–2,650 m. *D. cyanea* was also concentrated in this area (perhaps a site of unusually great or stable humidity for the region?). *D. coerulescens* extended from the same altitude up to the top of the mountain. Thus the only forms at the summit are *D. coerulescens* and *D. carbonaria brunneiventris*—a somewhat unusual combination in isolation.

The relations among members of the cluster on this hill differ from those of corresponding birds of the town and its outskirts. They are closer but less stereotyped in some respects. There are wide or complete overlaps of territories among *D. carbonaria brunneiventris, D. lafresnayii unicincta,* and *D. cyanea*, and between *D. carbonaria brunneiventris* and *D. coerulescens.* There are at least partial overlaps of territories between *D. cyanea* and *D. coerulescens* at middle altitudes. (Local preferences for particular strata of vegetation levels above ground, are conventional. *D. cyanea* is more arboreal than *D. carbonaria brunneiventris.*) Where the territories of different species overlap, reciprocal inhibition of songs is only intermittent. There are numerous breakdowns in all directions. I heard many cases of partial or complete synchrony of songs between *D. carbonaria brunneiventris* and *D. cyanea*, between *D. lafresnayii unicincta* and *D. cyanea*, between *D. coerulescens* and *D. carbonaria brunneiventris*, between *D. coerulescens* and *D. lafresnayii unicincta*, and, perhaps most frequent of all, between *D. carbonaria brunneiventris* and *D. lafresnayii unicincta*. This does not mean that there is no social discrimination. Despite the general sympatry and occasional synchrony of songs, there is good mutual avoidance on a small scale, much as at Quito and Cutervo. Different species do not usually come close together or visit the same places at the same times. The only unmistakable interspecific approach among diglossas that I saw on Tinaja was an attack by a *D. carbonaria brunneiventris* upon a *D. coerulescens*. I also saw a *D. cyanea* attacked by an *Aglaeactis cupripennis*, but this is less remarkable.

Brush-finches are so rare and inconspicuous around Chachapoyas that I was not able to study their interactions with diglossas.

The differences between the birds of Cutervo and Chachapoyas may be another indication that some of the peculiarities of populations are not strictly adaptations to immediate physical or climatic conditions.

Central Peru

This is another intermediate region. It is more conspicuously transitional than Chachapoyas. The degree or amount of intermediacy of social relations in the region as a whole may be roughly equivalent to that in the eastern and central cordilleras of Colombia, but the details are distinct. *In this southern region, there is usually less disorder or variability at any given point, but more differences between points, than in the most nearly comparable regions to the north.*

Forms of diglossas seen were *D. cyanea, D. carbonaria brunneiventris, D. lafresnayii pectoralis*, and *D. baritula* "*sittoides*." Other members of the cluster were *Conirostrum cinereum*, *Myioborus melanocephalus*, *Atlapetes schistaceus, A. torquatus*, and *Colibri coruscans*. Other species of interest included the hummingbirds *Metallura phoebe* and *Colibri thalassinus*, and the "warbler" or "tanager" *Hemispingus frontalis*.

Most of the areas that I visited in the region can be assigned to one or the other of two groups of sites. (1) The outskirts of the town of Tarma and the nearby villages of Chuchupampa and Huascé, ca. 2,850–3,400 m, and several stretches above and below the town of Palca, east of Tarma along the road to Maraynioc, ca. 2,400–3,100 m. (2) Various localities to the north in the general region of the city of Huánuco, i.e., hills above the town of Panao, ca. 2,500–2,550 m, and the area of Carpish Pass along the road to Tingo Maria, ca. 2,550–2,700 m. The neighborhood of Tarma has a dense human population, with many crop fields, hedges, some fruit trees, and much *Eucalyptus*. It does not appear to be extremely humid. The area of Palca is both more humid and less intensively cultivated on the average. At the times of my work there was some natural-looking scrub and forest left, especially in ravines and on steep slopes. The Carpish Pass area may be even more humid. It had extensive stretches of rich ''alpine'' and ''upper subtropical'' forest and scrub, as well as obviously young second growth. Some of the hills above Panao had patches of damp and lush vegetation, often in close proximity to crop fields.

The only honeycreepers seen at Tarma were *Conirostrum cinereum* and *D. carbonaria brunneiventris*. Both were common, the former perhaps even more so than the latter. Their habitat preferences were, as usual, broadly overlapping. Sometimes their territories were also partly overlapping. More often they were closely adjacent but nearly or completely exclusive. In either case, both forms showed excellent reciprocal inhibition of songs.

At lower altitudes near Palca the dominant form is *D. carbonaria brunneiventris*, and *C. cinereum* is relatively rare. Overlapping of territories may be usual here, with some mutual avoidance and social segregation as well as reciprocal inhibition. I did, however, see repeated attacks by *D. carbonaria brunneiventris* upon *C. cinereum* on a few occasions, and also a *C. cinereum* using a hole in a flower made by *D. carbonaria brunneiventris*.

Most of my work at higher altitudes above Palca was on a hill called Chutacocha. This area is inhabited by *D. carbonaria brunneiventris*, *D. lafresnayii pectoralis*, and *D. cyanea*. Again *D. carbonaria brunneiventris* is abundant. Both *D. lafresnayii pectoralis* and *D. cyanea* are rare. The territories of *D. cyanea* overlap those of both *D. lafresnayii pectoralis* and *D. carbonaria brunneiventris*. *D. cyanea* may approach the other forms quite closely without overt hostility. It may also sing at the same times. This might suggest that the local *D. cyanea* has dropped out or partly withdrawn from the main nexus of specialized diglossa relations. Interactions between *D. carbonaria brunneiventris* and *D. lafresnayii pectoralis* are more complex. *D. lafresnayii pectoralis* was found only in wet but rather open scrub at *ca*. 3,050 m. *D. carbonaria brunneiventris* was above and below and on all sides, and at times even in the same places. In April 1963 my attention was focused on a violent and prolonged interspecific dispute. At the beginning a single *D. lafresnayii pectoralis* was intruding upon the territory of a pair of *D. carbonaria brunneiventris*. In the course of the next week the *D. lafresnayii pectoralis* individual acquired a mate and the two of them took over the *D. carbonaria brunneiventris* territory almost completely. The process was accompanied by much fighting between the two species. *D. lafresnayii pectoralis* usually took the initiative, but the *D. carbonaria brunneiventris* fought back and sometimes launched attacks of their own. There also was much singing, with many overlaps of phrases. When I revisited the area in February of 1964 the situation had calmed down. Individuals and pairs *D. lafresnayii pectoralis* and *D. carbonaria brunneiventris* were sharing territories more or less peacefully, with mutual avoidance and reciprocal inhibition of songs, as do their relatives near Quito and Cutervo. It should be mentioned that *D. lafresnayii pectoralis* and *D. carbonaria brunneiventris* have different color patterns but surprisingly similar songs. For a form of the *lafresnayii* group, the songs of *pectoralis* are unusually *brunneiventris*-like, accelerated in effect.

There is another mix of diglossas in the Carpish Pass area. Here *D. lafresnayii pectoralis* is by far the most abundant form. I did not see a single *D. carbonaria brunneiventris* in the area, even though there was some scrub that looked suitable for the species. Perhaps in this area *D. lafresnayii pectoralis* has expanded to fill some of the habitats used elsewhere by *D. carbonaria brunneiventris* and other forms of *D. carbonaria*. The predominance of *D. lafresnayii pectoralis* may also illustrate another exclusion. Both Carpish Pass and the area preferred by *D. lafresnayii unicincta* on Tinaja, near Chachapoyas, are rather low in altitude for the species or species-group *D. lafresnayii*. These places recall some habitats of *D. albilatera* in Venezuela, Colombia, and Ecuador. It is possible that such races as *D. lafresnayii unicincta* and *pectoralis* have preoccupied some or all of a potential *D. albilatera* niche. This might help to explain why *D. albilatera* is confined to the northern Andes and does not extend farther south than extreme northern Peru. The only other diglossas seen at Carpish were a very few *D. cyanea* and one female of *D. baritula* "*sittoides*," all associated with mixed flocks. *D. cyanea* stuck to rather high levels in trees. They ranged over *D. lafresnayii pectoralis* territories in the courses of the wanderings. But I did not see any actual contacts between the two species, nor hear any overlaps of songs. The single *D. baritula* "*sittoides*" may well have been a stray from some lower, more open, or less extremely humid area.

Both the sites and the birds above Panao are more varied. Individuals and pairs of *C. cinereum* are common in low sparse scrub with scattered trees at relatively low altitudes, especially in the immediate vicinity of human settlements. Local *C. cinereum* does, in fact, seem to be largely commensal on man. In this respect it resembles its relatives of the Tarma and Chachapoyas areas, but differs from other members of the same species in the central cordillera of Colombia and the main mass of the central Andes. Some degree of commensalism is characteristic of several, perhaps most, kinds of conebills (see above and also Moynihan, 1968b). It is *C. cinereum* of the central Andes, not that of the south, that is unusual for the genus. *C. cinereum* of the immediate vicinity of human settlements at Panao does not have many opportunities to contact or interact with other honeycreepers. *D. baritula* "*sittoides*" also is common, but tends to be farther away from the town at slightly higher altitudes and in thicker scrub. The microgeographical and ecological segregation of *D. baritula* "*sittoides*" and *D. cinereum* in the general neighborhood of Panao seems to be remarkably clean and neat. There are few or no spatial overlaps between the two. They are much more definitely separated here than are the members of the same species (or species-groups) near Chachapoyas. *D. carbonaria brunneiventris* is less abundant near Panao than is either *D. baritula* "*sittoides*" or *C. cinereum*, but it is fairly densely aggregated in patches of particularly thick and tall scrub or low forest, again at relatively high altitudes. Territories of *D. carbonaria brunneiventris* and *D. baritula* "*sittoides*" may be adjacent, usually when *D. baritula* "*sittoides*" is peripheral to *D. carbonaria brunneiventris*, but they seldom overlap to any appreciable extent (only some *D. c. brunneiventris* trespass briefly). Perhaps surprisingly, I did see a few *C. cinereum* in *D. c. brunneiventris* areas. In these circumstances there was some overlapping of territories, with mutual avoidance; i.e., the relations between the two forms are not the same here as near Tarma. I did not see or hear any *D. lafresnayii pectoralis* above Panao. Presumably it was excluded by *D. carbonaria brunneiventris*—a sort of mirror image reversal of the result of competition at Carpish. Individuals and pairs of *C. cyanea* were found in many parts of *D. baritula* "*sittoides*" and *D. carbonaria brunneiventris* habitats, but they were scarce and widely scattered. They may have ranged through or over the territories of both *D. baritula* "*sittoides*" and *D. carbonaria brunneiventris*, but they seemed to prefer the tallest trees available, and I did not observe them to become involved in face-to-face encounters or interactions with any other members of the local cluster.

Reciprocal inhibition of songs is as good at Panao as in other areas of the region—or perhaps even better. Much more often than not it is nearly perfect among *D. cyanea*, *D. baritula* "*sittoides*", and *D. carbonaria brunneiventris*, and between these forms and any *C. cinereum* that is close enough to hear and be heard. It also extends to other species of other systematic groups.

There is another habitat of the southern Andes that is very cold indeed, and should perhaps be considered part of the humid zone, but is nevertheless peculiar. It is provided by *Polylepis* "woods." *Polylepis* trees are of moderate size and occur at very high altitudes, higher than any other of the local trees. They form what are presumed to be natural clumps at some places. They also are planted as hedge-like windbreaks. Patches of *Polylepis* are remarkably uniform, monotonous, and impoverished; not only are other kinds of trees lacking, but there are very few bushes or other forms of low vegetation, apart from a few grasses, mosses, and ferns. The fauna in these patches is correspondingly simple and much more impoverished than in other forests and scrub of the humid cold zone.

In July 1974 I made two brief visits to small stands of *Polylepis* in central Peru near the village of Quishá, around 3,900–4,000 m, approximately halfway between Huánuco and the town of La Unión to the west. The only honeycreepers found were two conebills: *C. cinereum* and the so-called Giant Conebill—not really very large—*Oreomanes fraseri*.

Oreomanes is supposed to be confined to *Polylepis*. It seems to be rare.

The few individuals that I saw were associating with distinctive mixed flocks of flycatchers and finches of the genera *Phrygilus* and *Catamenia*. These groups are very different, in composition and appearance, from the mixed flocks of tanagers, warblers, brush-finches, etc., described below. They will not be considered further in this paper.

C. cinereum, on the other hand, was relatively common. Perhaps again as a commensal of man, but apparently not as a member of mixed flocks.

As far as I could tell, both conebills were purely insectivorous during the periods of my visit. They gleaned insects from the same leaves and twigs. They did not, however, seem to pay any attention to one another. Unfortunately, they were not singing at these times, but they did not join, avoid, or fight with one another.

The rather small hummingbird *Metallura phoebe* was seen near Palca and Carpish Pass. It visited and probed the holes made by diglossas (almost certainly *D. carbonaria brunneiventris*) in large tubular flowers such as *Passiflora* (pink in this region). It usually avoided contact with the honeycreepers, but below Palca I saw one *Metallura* make repeated sweeps upon a *D. carbonaria brunneiventris* until the infuriated victim turned and drove its tormentor away. There were many other small hummingbirds around that I could not identify. A female or juvenile of one species, perhaps an *Eriocnemis*, was seen to attack a male *D. baritula "sittoides"* in the same general area. A few individuals of what appeared to be a species of *Aglaeactis* (*castelnaudii*?) were also found near Panao. They seemed to ignore other nectarivores.

Colibri coruscans is more or less common and widespread near Panao, and also occurs at Tarma. It appears to be a partial but real member of the diglossa cluster in this region. As usual, it occupies many of the same kinds of habitats as the local diglossas. Its territories seem to overlap or be overlapped by those of some *D. cyanea*, but they are more likely to be merely adjacent to those of *D. carbonaria brunneiventris, D. baritula "sittoides,"* and *C. cinereum*. Local *C. coruscans* is not usually actively aggressive toward diglossas. Only occasionally does a *C. coruscans* trespass to threaten or to attack a *D. baritula "sittoides"* (*D. baritula* seems to be subordinate, at the bottom of the hierarchy, here as in other regions, such as in the eastern cordillera of Colombia). Vocal behavior is even more revealing. Local *C. coruscans*, like members of the species elsewhere, sings persistently and at length. It also, however, shows signs (or unusually strong signs) of being affected by reciprocal inhibition. At Panao at least, its songs did not overlap those of other members of the cluster as frequently as would have been expected. Some interactions with *C. cyanea* were particularly interesting. Individuals of the two species often alternated songs when they were close together, but usually did not mind overlapping when they were far apart. Presumably acoustic interference at a distance is not significant for them.

A concentration of *Colibri thalassinus* was found ca. 2,500 m near Panao in an area of thick low scrub. These birds were aggressive. They attacked other and smaller hummingbirds passing by. Their songs overlapped those of both *D. carbonaria brunneiventris* and *C. cyanea*, but I did not see any actual attacks upon diglossas. There were no *C. coruscans* in the immediate area. *C. coruscans* and *thalassinus* may be mutually exclusive in this region, perhaps even more definitely segregated than on Sierra Nevada de Santa Marta.

The whitestarts and brush-finches of the region certainly are integrated into the diglossa cluster. *Myioborus melanocephalus* and *Atlapetes schistaceus* are numerous in the more humid areas. The territories of both species overlap those of diglossas and *Colibri coruscans* (and *Conirostrum cinereum* in a few cases), but both are usually careful to arrange their songs to reduce or avert synchrony between themselves and with other full or partial members of the cluster. A third species, a tanager-like warbler or warbler-like tanager, *Hemispingus frontalis*, may have some similar relations. At Carpish, *H. frontalis* songs tended to alternate with those of both *M. melanocephalus* and *D. baritula* "*sittoides.*" Another brush-finch, *Atlapetes torquatus*, seemed to be involved in the corresponding web at Panao.

The Panao situation may represent a maximum. In this general area the reciprocal inhibition of songs extends to 6-8 species, viz., certainly *A. schistaceus* and *M. melanocephalus*, probably *C. cinereum* and *A. torquatus*, and partly *C. coruscans*, in addition to *D. carbonaria brunneiventris*, *D. baritula*, and *D. cyanea*. It seems unlikely that such a system could accommodate more species.

There may, nevertheless, be still other possible or potential components of the cluster at less crowded sites. The small tanagers or warblers *Thlypopsis ornata* and *T. pectoralis* might be examples. These species were seen in several areas. At least once, below Palca, a single *T. pectoralis* was attacked and supplanted by a *D. carbonaria brunneiventris*. This may have been nothing more than an expression of the usual bad temper of the species *D. carbonaria*, but it was suggestive because a *T. ornata* was seen to visit and probe diglossa holes in flowers in central Ecuador (Moynihan, 1963a). Perhaps *Thlypopsis* spp. compete with diglossas for food as well as space and other resources.

Obviously the interspecific behavior patterns of the members of the diglossa cluster of this region are complex and heterogeneous. They cannot be summarized in a few phrases. For comparison with other intermediate regions of the northern Andes, however, it may be sufficient to say that central Peru is characterized not only by widespread reciprocal inhibition of songs and considerable microgeographical and ecological isolation on a small scale, but also by surprisingly frequent and recurrent tendencies toward territorial exclusiveness. This might be called "micro-microgeographical" separation on a relatively tiny scale, even in similar or identical habitats and among forms that are not particularly similar to one another in outward appearance, in color or shape, or in voice.

SOUTHERN PERU

Forms of diglossas seen: *D. cyanea*, *D. coerulescens*, *D. carbonaria brunneiventris*, *D. baritula* "*sittoides*," and probably also *D. lafresnayii* *albilinea*. Other members of the cluster were: *C. cinereum* and *Poospizopsis caesar*. Other probably or possibly relevant species were: *Colibri coruscans, C. thalassinus, Myioborus melanocephalus, M. miniatus, Atlapetes schistaceus, A. tricolor.*

In this region I worked near the city of Cuzco, the pre-Columbian ruins of Machu Picchu to the north, and several intervening settlements in the valley of the Urubamba River, i.e., Pisac, Calca, and the town of Urubamba.

The Cuzco-Pisac-Calca-Urubamba observations may be considered as a unit. These areas have large human populations and have been subjected to intensive cultivation for many centuries. They are only moderately humid, verging on the semiarid in some places. I worked at altitudes between approximately 2,780 and 3,250 m, in a variety of habitats, ranging from hedges with introduced trees to lush and variegated scrub. Some sites were moderately rich in flowers and hummingbirds, but all were poor in members of the diglossa cluster during the periods of my visits. I found a few *C. cinereum*, mostly in hedges and thin scrub and eucalypts, and *D. carbonaria brunneiventris*, mostly in thicker scrub, but no other diglossas.

Perhaps this poverty is a result of too many clearings of vegetation. *C. cinereum* and *D. carbonaria brunneiventris* were so scarce that I saw few reactions between them. Probably they show reciprocal inhibition of songs and territorial exclusiveness here, as in most other southern parts of the cold tropical zone of the Andes.

Another species, *Poospizopsis caesar*, occurs in many of the same areas and habitats near Cuzco, Pisac, etc., and is more common. It is technically a "finch," but it is rather thin-billed and looks very much like a large conebill. Adults are gray above, with white eyebrows and throat, rufous breast, gray flanks, white belly, and rufous undertail coverts. The song of the species is a twitter, reminiscent of both *D. lafresnayii pectoralis* and some *Conirostrum cinereum*. It tends to skulk and to stay low in scrub. Unfortunately, I could not tell what it was feeding on. Probably it is partly insectivorous. It might even be occasionally nectarivorous and/or feed on flower buds or soft fruits. In any case, it seems to have become a full member of the local diglossa cluster in its social reactions. Its territories tend to be exclusive, not overlapping those of either *D. carbonaria brunneiventris* or *C. cinereum*. It fits into the reciprocal inhibition of song complex. Its phrases also tend to be nonoverlapping.

Possibly *Poospizopsis* is really central to the cluster in these areas. It has already been mentioned that at any given place some species usually contribute more to the maintenance of the system than do others. The central and connecting role is often played by forms of *D. carbonaria*. In the impoverished areas of southern Peru, however, it seems likely that *Poospizopsis*, the most abundant of the relevant species, is the only one that can do the job. Perhaps it has ousted *D. carbonaria brunneiventris* from its original role as the environment has been changed and degraded.

The area of Machu Picchu is not far from the town of Urubamba, but it presents a rather different aspect. It is obviously more humid on the average.

It also was less impoverished at the times of my observations. I worked on the mountain of Machu Picchu itself, from approximately 2,400 to 2,900 m, and on the adjacent, smaller but more precipitous peak of Huayna Picchu, ca. 2,500–2,600 m. The local habitats include sparse scrub on the rocky sides of Huayna Picchu, great expanses of dense second-growth with much bamboo and occasional trees on the western and northwestern slopes of Machu Picchu, very lush, tall and natural-looking "upper subtropical" forest on the eastern and southeastern slopes, and a small patch of "alpine" scrub at the top of the mountain. Because of the topography of the area, I was not able to make as extensive observations on the eastern slopes as on the western ones.

Diglossas are more abundant at Machu Picchu than near Cuzco, but still less common than in some other regions. Some forms of the local cluster are widely distributed within the area. I found individuals and pairs of *D. cyanea* almost everywhere I went. *D. carbonaria brunneiventris* was dominant on most of the western slopes, but may not have reached the very top. Both *D. baritula* "*sittoides*" and *C. cinereum* were found in smaller numbers on the same slopes from approximately 2,400 to 2,700 m. *C. cinereum* also occurred on Huayna Picchu. These various forms showed their usual slightly different habitat preferences, but two or three were often at the same or closely adjoining sites. There were many broad overlaps of territories, but contacts and interference between individuals of different forms were held to a minimum by rather careful mutual avoidance, and also reciprocal inhibition of songs. Social segregation may be more consistent and effective on Machu Picchu than in some other southern parts of the humid cold zone.

It is not necessarily the only system available or used. I saw and heard *D. coerulescens* only twice; both times in the scrub at highest altitudes. The local representatives of *D. lafresnayii* are even more obscure. Specimens of *D. lafresnayii albilinea* were collected on Machu Picchu by earlier workers. I heard only a few snatches of appropriate songs and caught two glimpses of individuals which may have belonged to this form at moderate elevations, ca. 2,500–2,600 m, on the western slopes of the mountain near concentrations of *Passiflora*. Perhaps both *D. lafresnayii albilinea* and *D. coerulescens* are partly segregated ecologically and/or microgeographically.

The behavior of the local whitestarts and brush-finches seems to be entirely conventional.

Hummingbirds are particularly flourishing on Machu Picchu. They may be almost as abundant here as in the southern part of the western cordillera of Colombia. The most distinctive feature of the Machu Picchu area is an enormous proliferation of *Colibri*, both *coruscans* and *thalassinus*. There is little obvious ecological difference between the two species here. Both occur in a wide range of habitats and elevations, although *C. thalassinus* was found to be most numerous at slightly lower altitudes than *C. coruscans* on the western slopes, and also (surprisingly) to extend farther, or more successfully, into the forests of the eastern slopes. The territories of the two species were usually mutually exclusive, but both overlapped those of the diglossas and their associates apparently at random. Both species seemed to ignore the local diglossas. They showed few or no signs of reciprocal inhibition of songs either with one another or with other species.

I saw only three unmistakable interspecific attacks: one by a *C. thalassinus* upon a *coruscans*, one by a *thalassinus* upon a *cinereum*, and one by an unidentified smaller hummingbird upon a *cinereum*. *D. baritula* "*sittoides*" seems to be relatively fortunate here!

Northern Bolivia

This is very close to the southern end of the life zone with which we are concerned.

Forms of diglossas seen: *D. cyanea, D. carbonaria brunneiventris, D. c. carbonaria, D. lafresnayii mystacalis*, and *D. baritula* "*sittoides*." Other members of the complex are: *C. cinereum* and possibly *C. ferrugineiventre*. Other relevant species are: *Myioborus melanocephalus* and *Atlapetes rufinucha*, and possibly also *Atlapetes torquatus, Thlypopsis ruficeps* and *Colibri coruscans*.

I paid special attention to two series of areas in this region: in La Paz, and in the *yungas* to the east, near the town of Unduavi (approximately 50 km from La Paz) on the road to Coroico. La Paz itself is a large city of generally rather dry climate. It is one of the highest cities in the world, but sprawls over steeply descending slopes. Most of my work was done in gardens of the neighborhood called Miraflores and some of the lower parts of the city extending toward the suburb of Obrajes, between 3,675 and 3,450 m. These gardens are irrigated or watered regularly and contain many exotic trees, shrubs, and flowering plants, including even north European forms such as roses, but they provide excellent habitats for many native birds, including some that are adapted to more or less extremely humid conditions. The *yungas* are naturally wetter and also less modified by human activities. They are separated from La Paz by an intervening stretch of very high and barren ground, *altiplano*, puna, and bare or snow-covered rock. Then they descend gradually and irregularly to the east. I worked from the very beginning of the descent above Unduavi, in patches of rather sparse scrub, at ca. 3,450 m, down to and past Unduavi with its gardens, hedges, and crop fields, and farther along the road to Coroico into an area of varied vegetation with much second-growth, at ca. 2,850 m. I also made observations along a side road to Cillutinarca which passed through "alpine" scrub interspersed with patches of puna, bogs, and small lakes at ca. 3,450 m. This last area is almost excessively humid. It is probably as wet as any other place I visited in the Andes. Although there is no direct link of forest or scrub between the *yungas* and La Paz, there is an indirect or partial connection to the north, toward the towns of Calocoto and Palca and on the slopes of the volcano Illimani. I did a little supplementary work along another road here, in second-growth and scrub, especially around the village of Ovejuyo. My altimeter was broken, but the area cannot be much lower than the lower parts of La Paz.

It seems to be characteristic of northern Bolivia that there is only a single predominant member of the diglossa cluster in any given area. In the gardens of La Paz the predominant form is *D. c. carbonaria*. It is very abundant. The only other form is *Conirostrum cinereum*. It is not rare, but it is much less common than its rival diglossa. It also tends to play a subordinate social role. The territories of *C. cinereum* and *D. c. carbonaria* are often broadly overlapping in the more thickly planted gardens. In these circumstances the conebills make visible efforts to keep away from the diglossas. I saw a substantial number of attacks by *D. c. carbonaria* upon *C. cinereum*. Sometimes the attacks lead to long chases. Doubtless there is also considerable ecological overlap between the two species, here as elsewhere. *C. cinereum* often feeds in the same places or kinds of places as *D. c. carbonaria*. But it also shows a conspicuous tendency to go high in trees, especially eucalypts, and to remain there for comparatively long periods. The *C. cinereum* of La Paz seem to have carried the arboreal tendencies of the southern populations of the group to an extreme. Perhaps they are using trees as refuges from *D. c. carbonaria*. The songs of the two forms usually do not overlap. There is some inhibition in force. Perhaps it is not entirely reciprocal in this case. *C. cinereum* may be more inhibited by *D. c. carbonaria* than vice versa. The mere sight of *D. c. carbonaria* may be enough to cause a singing *C. cinereum* to cease. In sparser or less heavily planted gardens the territories of the two forms may be more often adjacent and exclusive than overlapping, but many of the same social constraints seem to apply.

D. c. carbonaria is also aggressive toward other species. I saw it attack *Colibri coruscans* and even, once, the relatively enormous hummingbird *Patagona gigas*.

At the highest altitudes along the road to Cillutinarca, the only diglossa, perhaps the only real member of the cluster, is *D. lafresnayii mystacalis*. It is abundant throughout all the natural-looking scrub and in the adjacent second-growth.

The situation is more complex at slightly lower altitudes around Unduavi, at the base of the road to Cillutinarca, and along the road to Coroico. The predominant form here is *D. carbonaria brunneiventris*. It shows the expected habitat preferences in scrub, forest edges, and some gardens. There is a small but fairly dense population of *C. cinereum* in Unduavi and its immediate vicinity. These birds may be the result of a recent invasion; Niethammer (1956) does not record the species from this area. Evidently *C. cinereum* of northern Bolivia is as dependent upon the presence of man and his works as are other populations of the species in other regions of the southern Andes. The Unduavi birds tend to remain fairly low in gardens and hedges. They were seen in trees less frequently than their relatives of La Paz; presumably partly because tall trees were rare in the town itself and partly because *D. c. carbonaria* is absent from the area. A few kilometers to the east and slightly above Unduavi, the local fauna includes a moderate number of *D. carbonaria brunneiventris* and very few *C. cinereum* and *D. lafresnayii mystacalis*. Both the latter may be strays. Still farther to the east and lower, there are *D. carbonaria brunneiventris* and *D. cyanea*. The latter are also conventional in their habitat preferences. The relations among these forms are varied. At Unduavi the territories of *D. carbonaria brunneiventris* and *C. cinereum* can be either overlapping or mutually exclusive, but I never saw any contacts or heard overlaps of songs of the two species. To the east, where both *C. cinereum* and *D. lafresnayii mystacalis* may occur in the same kinds of habitats as *D. carbonaria brunneiventris*, the first two species are so rare, and perhaps transitory, that I could not do much with them. I never saw or heard any significant interactions among the three forms. Farther east the territories of *D. carbonaria brunneiventris* and *D. cyanea* are often broadly overlapping. The two species are usually kept apart by their preferences for different levels of vegetation and some degree of social segregation. I did, however, see an attack by a *D. carbonaria brunneiventris* on a *D. cyanea*, and heard some synchronous singing. Local *D. cyanea*, like some other southern populations of the species, may be partly or intermittently detached from the cluster.

At Ovejuyo I saw only a few *D. carbonaria* and *C. cinereum*, and one female *D. baritula* "*sittoides*." The latter may have been another stray. The territories of *D. carbonaria* and *C. cinereum* were adjacent and apparently exclusive, but intermingled in mosaic fashion. The territory or home range of the female *D. baritula* "*sittoides*"overlapped those of both *C. cinereum* and *D. c. carbonaria*. *C. cinereum* tended to stay high in the few trees that were available, higher than either of the other two forms. *D. c. carbonaria* occasionally attacked the female *D. baritula* "*sittoides*" but *C. cinereum* seemed to ignore her. *D. c. carbonaria* and *C. cinereum* alternated songs. I did not hear the *D. baritula* "*sittoides*" utter anything except alarm and call notes (perhaps females of this species never sing in ordinary circumstances). There were also some *Colibri coruscans* present. Their territories overlapped all the others. They fed on some of the same red, tubular flowers as *D. c. carbonaria*. They usually probed the flowers directly from the front in the typical hummingbird manner, but at least one individual was seen to put its bill to diglossa holes at the bases of corollas. The *C. coruscans* fought furiously among themselves from time to time. It is suggestive, therefore, that there were well-developed avoidance reactions between *C. coruscans* and some of their actual or potential competitors. I never saw an approach, much less a fight, between a *C. coruscans* and a diglossa or *C. cinereum* in this area. It is also possible that the *C. coruscans* were partly involved in the reciprocal inhibition of songs system. This may be another area in which *C. coruscans* has joined the cluster.

I add a qualification at this point. There is, or has been, some introgression, i.e. interbreeding, between *D.c. carbonaria* and *D.c. brunneiventris* in northern Bolivia. It is not, however, entirely free. Most individuals look like one form or the other. I have, in the preceding pages, called individuals by the names of the typological forms that they most resembled. This probably is valid on ecological grounds.

A further complication is added by the conebill *C. ferrugineiventre*. This species is roughly equivalent to *C. rufum* of the northern Andes. Pairs and small (family?) groups were seen in most of the higher altitude areas near Unduavi, in both lush, very humid habitats and more open and somewhat drier scrub. The species does not appear to be very abundant. It is certainly much less common than are *D. c. brunneiventris*, *D. c. carbonaria*, or *D. lafresnayii mystacalis* in their respective areas. The pairs and groups are scattered and highly mobile. Most of the *C. ferrugineiventre* seen were travelling with mixed flocks, like *C. sitticolor*, but I also found some that were quite alone, apparently without associates. The territories of the ''nongregarious'' *C. ferrugineiventre* were adjacent to those of *D. c. brunneiventris* and overlapping those of *D. l. mystacalis* in different areas. I did not see any close contacts between these conebills and either of the other species. The *C. ferrugineiventre* were careful to respect the rules of reciprocal inhibition of songs. It is possible that they take the place of *C. cinereum* away from human habitations.

My work in northern Bolivia occurred at a relatively early stage of this study. At that time I was not fully aware of all the possible connections between diglossas and other birds. Thus I did not pay as much attention to the subject as I should have. It is, nevertheless, my impression in retrospect that such birds as *Myioborus melanocephalus* and *Atlapetes* spp. probably are partial members of the cluster in northern Bolivia, in the same ways as in other regions of the Andes.

The ecological relations among different kinds of brush-finches are not always obvious. They deserve further investigation. In many sections of the Andes, the densest and most humid habitats are more or less reserved for members of the *A. schistaceus* species-group, while more open or drier scrub is the characteristic environment of *A. rufinucha*. In the parts of northern Bolivia that I visited, however, the *A. schistaceous* species-group is absent, and *A. rufinucha* occupies both niches. Whatever the reasons for this development, it is evident that some of the Andean species of *Atlapetes* have almost equal potential, like their neighbors, rivals, and partners, the diglossas of the same life zone.

Partial Summary

The mass of detail in the preceding descriptions may be reduced to a few general statements of trends and conditions. At the southern end of the western cordillera of Colombia there are relatively few contacts or overlaps among members of the diglossa cluster. The different habitat preferences of the different species tend to keep them apart by a form of microgeographical separation. In other regions of the northern Andes there also are specific habitat preferences, but they are less neat and less effective as barriers. There are numerous ecological and territorial overlaps and close contacts between species. These reach their maxima in the eastern and central cordilleras of Colombia. In the main section of the central Andes, i.e., in Ecuador and northern Peru west of the valley of the Marañón, different species occur in the same places very frequently, but are kept apart by social segregation. In the southern third of the cold humid tropical zone the situation is a distorted mirror image of the north. There are many overlaps and contacts in central and southern Peru, somewhat mitigated or complicated by an emphasis on interspecific territoriality. Microgeographical separation on a different scale, with increased or neater ecological distinctiveness, reappears in northern Bolivia in a form reminiscent of the western cordillera of Colombia.

Notes on Central America

The mountains of Central America resemble the Andes in many physical, climatic, and biotic features. They also are divided into "islands." There is one block of highlands in Costa Rica and the province of Chiriquí in western Panama. There is another block in Chiapas in southern Mexico, Guatemala, and adjacent parts of Honduras and El Salvador. North of the Isthmus of Tehuantepec, the highlands of Oaxaca and central Mexico extend to the main mass of the Rocky Mountains. Biotic links to South America, and tropical characteristics in general, are strongest in the Chiriquí-Costa Rica region, less evident in the Chiapas-Guatemala region, and gradually fade out to the north in the mountains of central Mexico.

There are no montane conebills in Central America, and only one stock of diglossas, with two main types: *D. baritula plumbea* in Chiriquí and Costa Rica, and several more subspecies in Mexico and Guatemala that can be subsumed under the name of "*baritula*."

Skutch (1954), Colwell (1973), and Wolf (1969) describe some aspects of the behavior and ecology of *D. baritula plumbea* in Costa Rica. I saw a few individuals of this form near the town of Cerro Punta in Chiriquí at ca. 1,820–2,100 m. Skutch also observed "*baritula*"; in Guatemala. Lyon and Chadek (1971) discuss certain reactions and relations of Mexican birds.

Some of the preferences and perhaps even the mere presence of *D. b.* "*baritula*" and *D. b. plumbea* in Central America are surprising. They are close relatives of "*sittoides*." Yet they often occur in rather different kinds of places. All the various "*sittoides*" seem to occur most frequently in areas that are semiopen and relatively dry for the cold humid tropical zone. The areas in which *D. b. plumbea* has been observed seem to be wetter on the whole, extremely wet in some cases; according to Skutch, so are the areas preferred by "*baritula*" in Guatemala. Such as it is, the available evidence suggests that the "*baritula*" and *plumbea* in Central America occupy niches that correspond more closely to those of *D. albilatera*, *D. carbonaria*, and/or *D. lafresnayii* of the Andes than to those of "*sittoides*." This is another example of the plasticity of diglossa types, and of their potential interchangeability or ability to play different roles (sometimes one another's roles) in different areas and conditions.

The current distributions of "*sittoides*," *plumbea*, and "*baritula*" imply earlier movements over considerable distances. Early members of the stock probably had to cross a wide gap of lowlands, and/or a marine strait, in the region of what are now the Darién of eastern Panama and the Chocó of extreme northern Colombia. The extensive nature of the radiation of diglossas in the Andes and the Guiana Highlands would suggest that the movement is more likely to have gone from South America to Central America than vice versa. If so, it is remarkable that the transit was not made by *D. albilatera*, humid adapted and often abundant at only moderate altitudes, or by *D. carbonaria*, so much more successful than *D. baritula* throughout most of the Andes; but there may be a simple behavioral explanation of the apparent anomaly (see below).

Populations of *plumbea* and "*baritula*" are usually minor elements in their local avifaunas. Much more important are hummingbirds, the only really major group of nectarivorous birds in the mountains of Central America, where they have speciated, diversified, and proliferated widely, although never to quite the same extent as in the larger and higher Andes.

Central American diglossas are known to be threatened and attacked by a variety of hummingbirds. Lyon and Chadek (1971) say that *Lampornis clemeciae* and *Eugenes fulgens* often direct threat displays at *D. b. "baritula."* Colwell (1973) says that *D. b. plumbea* is attacked by *Colibri thalassinus*. Central American populations of this latter species may be as generally aggressive as their South American cousins. Colwell notes that Costa Rican *C. thalassinus* fight furiously among themselves (see also Skutch, 1967) and with the larger hummingbird *Panterpe insignis*. According to Wolf (1969) and Wolf and Stiles (1970), *P. insignis* shows hostile behavior toward *D. b. plumbea* with varying effects. Sometimes the hummingbirds are able to drive away the diglossas, sometimes not. The results seem to depend upon the availability of alternative food sources. Skutch (1967) describes attacks by a nesting female *Lampornis calolaema* (often considered conspecific with *L. castaneoventris*) upon a nest-building female of *D. b. plumbea* in Costa Rica. I saw many, more or less inhibited, attacks by a female of the same species (or possibly *L. castaneoventris*) upon both sexes of *D. b. plumbea* feeding on *Fuchsia* bushes in a garden below Cerro Punta in Chiriquí. This appeared to be simple defense of food rather than an expression of individual or specific antagonism. The female *Lampornis* stopped attacking the diglossas as soon as they left the *Fuchsia*, even when they remained in plain sight. She also swooped at and chased away tiny hummingbirds, presumably *Lophornis delattrei*, whenever they visited the same plants.

4

ADAPTIVE STRATEGIES OF NECTARIVOROUS BIRDS

Adaptive strategies may be analyzed at the levels of the individual, species, or group, in ecological or ethological terms. Colwell (1973), for instance, discusses feeding ranges of some species of Costa Rican hummingbirds. He classifies *Eugenes fulgens* as an ''interstitial'' form. It feeds in between and beyond the territories and foraging hours of its most important competitors. *Panterpe insignis* is an opportunistic generalist. The term is self-explanatory. *Colibri thalassinus* is a sequential specialist in Costa Rica, seasonally moving up and down the mountains and tending to concentrate on one or a very few types of flowers at any given time.

The same categories can be recognized in South America. Among the diglossas, *D. cyanea* and *D. lafresnayii* and most (if not all) populations of *D. carbonaria* are opportunistic generalists. As noted above, some Andean hummingbirds such as *Aglaeactis cupripennis* can be sequential specialists. *Colibri thalassinus* may be as mobile in the Andes as in Central America. This might help to explain why my observations of the species were so sparse and unsatisfactory.

Colwell suggests that *D. baritula plumbea* is ''interstitial.'' So are all or most South American populations of the same species-group—but only in one sense. The interstitial category is heterogeneous. There are species that depend upon foods or other items that are widely scattered among or between the vital resources and territories of dominant competitors. Such species may have to trapline from site to site over wide areas. This might be called ''geographical'' or ''topographical interstitiality.'' Other birds may use resources that are more evenly distributed or concentrated within the territories or home ranges of their rivals, but approach them at times or in circumstances when competition is reduced or weakened. This might be called ''behavioral interstitiality.'' A single species or population may combine the two strategies (*Eugenes fulgens* of Costa Rica would seem to be an example) but there is no logical or practical reason why the two methods of earning a living should not be separated in individual or specific cases.

It is possible that some of the less frequently seen members of the diglossa cluster(s) of the Andes such as *D. coerulescens*, *C. rufum*, and *C. ferrugineiventre* are topographical interstitialists. *D. baritula ''sittoides''* is different. The flowers and probably the arthropods on which members of this group feed are numerous, diverse, and (as a whole) common over large expanses of the Andes. *D. baritula ''sittoides''* is only behaviorally interstitial insofar as it can avoid attacks by larger and more aggressive birds by retreating within the fine meshes of the centers of bushes where many competitors cannot follow (see the account of the eastern cordillera of Colombia).

At least one other small diglossa, *D. albilatera*, is also behaviorally interstitial, but it seems to be less immediately resilient. *D. albilatera* seems to be more easily discouraged by attacks, or remains discouraged for longer periods on the average, than *D. baritula "sittoides."* It may use the same evasive tactics, take refuge within or behind thickets and tangles; but it does not, in my experience, usually return and expose itself to renewed aggression as rapidly or repeatedly. This contrast is correlated with the different habitat preferences of the two forms. *D. baritula "sittoides"* is adapted to less covered sites. It probably must come out into the open frequently in order to get sufficient food. *D. albilatera* is adapted to denser vegetation. It probably sacrifices less by remaining hidden longer. It may be able to get quite a lot of food in its more numerous and extensive thickets and tangles. *D. baritula "sittoides"* has to be undiscourageable, while *D. albilatera* can afford to be more skulking, prudent, and cowardly.

A combination of boldness and a willingness to take risks, with effective evasive tactics, might well be advantageous in many new and problematic situations, in new areas and with strangers.

Thus, it would seem that interstitiality per se is not necessarily much of a help or encouragement to range expansion, but that some of the behavioral adaptations to a certain kind of interstitiality can be useful preadaptations. Somewhat paradoxically, the resilience that may be supposed to have been evolved by the ancestor of the *D. baritula* group to cope with openness in South America could also have been the crucial factor that later permitted the stock to invade and occupy more closed habitats in Central America.

It would be interesting to know if in their new environment *D. baritula plumbea* and "*baritula*" have become more prudent than South American "*sittoides*." My own brief observations of Panamanian *D. b. plumbea* would suggest that the answer is "yes."

Strategies at the level of the systematic or phylogenetic group have to be discussed in more general terms. Granted that closely related birds may have some different preferences and techniques, and distantly related birds similar preferences and techniques, it is still possible to recognize certain basic aspects or elements of strategy that are shared by all or most members of a group and not by members of many or most other groups. Of course, these basic elements, especially as they are reflected in anatomy or morphology, may be the criteria by which the groups are defined.

The majority of nectarivorous birds in the New World tropics fall into four groups: hummingbirds, diglossas, the conebills and the Bananaquit, and the brilliant blue and green honeycreepers of the genera *Dacnis*, *Chlorophanes*, and *Cyanerpes* (perhaps a tribe Dacnini). Hummingbirds are everywhere in the Neotropics. The other groups have more restricted distributions. An understanding of their basic strategies may help to explain the restrictions.

Nectar is a good source of energy, easily assimilated and mobilized; but it is not without drawbacks. It must be supplemented by other foods, usually small arthropods, for some essential nutrients. It is not visible or detectable as such at a distance. A bird has to visit and, usually, probe a flower in order to determine if nectar is present in profitable amounts. Flowers have complex distributions in space and time, and may be difficult to find. The nectars of some kinds of flowers can be extracted only by special methods that may be elaborate and time-consuming.

There have been excellent studies of the digestive physiology and time-and-energy budgets of hummingbirds, e.g., Berger (1974), Hainsworth (1974), Hainsworth and Wolf (1972), Lasiewski (1963), Pearson (1950), Stiles (1971), Wolf and Hainsworth (1971), Wolf, Hainsworth, and Gill (1975), and Wolf, Hainsworth, and Stiles (1971). It is obvious that hummingbirds are more varied than any other group of nectarivorous birds. Different species have bills of different sizes and shapes, short or long, straight or strongly curved, all as adaptations to probing different kinds of flowers. All hummingbirds, however, have unique flight control, tend to be very active, and have very high metabolic rates when active. With their many specializations they may be very efficient at getting a large quantity of nectar rapidly, but they must expend a great deal of energy in doing so.

As far as I know, the physiologies and budgets of other New World nectarivorous birds have not been studied in detail or quantified. There has been recent work on African sunbirds of the family Nectariniidae (see Gill and Wolf, 1975a and 1975b, and Wolf, 1975, in addition to some of the references cited above). Sunbirds are more closely related phylogenetically to honeycreepers than to hummingbirds; but they may be quite close to the latter ecologically. They also seem to have specialized in getting much nectar rapidly at a rather high cost.

The dacnine honeycreepers are more generalized. They have bills of short to moderate length, straight or only slightly curved, and normal powers of flight. Many or all of them take substantial amounts of animal food, or at least spend considerable time searching for it. They tend to visit flowers at longer and more irregular intervals than do hummingbirds. They may be less efficient in obtaining nectar than are hummingbirds, but they must expend less energy in the process.

Much the same can be said of diglossas. Their principal distinction is their ability to cut into flowers. The Dacnini cannot, or usually do not, do this. Flower-piercing takes time and may be laborious. It probably entails a greater expenditure of energy than any nectar-feeding techniques of other honeycreepers.

The ranges of diglossas and Dacnini, as groups, are remarkably exclusive. There are no really lowland diglossas, and few or no montane Dacnini. Representatives of the two groups may meet in the hills, but overlaps among them must be slight or narrow in most places. I never saw dacnine honeycreepers in areas inhabited by diglossas in the Andes, or even at moderate elevations in Chiriquí.

It would appear that there are opportunities for two basic ecological types of nectarivorous birds in many life zones of the Neotropics: species (hummingbirds) that obtain high yields at high costs, and other species that obtain lower yields at lower costs. The two ecological types can coexist. But the two major groups that have adopted the low yield/low cost strategy seem to be incompatible. They replace one another altitudinally.

The incompatibility and the replacement need to be explained. These must, I think, be related to differences in feeding techniques and the distribution of flower forms. I am not aware of any reliable figures on the subject; but it is my impression that flowers with long tubular corollas are *relatively* more common in humid forest and scrub at high altitudes than in the most nearly similar habitats in the lowlands, viz the difference between the lowland and highland species of *Passiflora* mentioned above. The advantages of long tubular flowers for highland plants could be various. The shape could facilitate conservation of heat, shield parts of the flower from rain, and/or provide protection against clumsy movements of pollinators by canalizing and restricting their lines of approach. Both hummingbirds and bees average larger, and may therefore be clumsier, in the highlands than in the lowlands. Birds are the more likely of the two to be relevant to the plants considered here. Most of the tubular flowers in the highlands are red, pink, or orange, colors visible and attractive to birds. Cruden (1972) has already noted that birds are more effective pollinators than bees in the wet parts of the mountains of Mexico.

Long tubular flowers can be exploited by only certain kinds of birds, diglossas and long-billed hummingbirds (and parasites and commensals—see below). Other flowers are available to, and potentially utilizable by, all birds, including Dacnini. Probably flowers that could be used by Dacnini are simply too rare in the mountains to permit populations of honeycreepers of this type to survive in competition with diglossas and other birds that have access to both the same food sources and other (reserved) supplies. In the lowlands, on the other hand, there are undoubtedly enough flowers to permit Dacnini to survive and flourish. Diglossas must be at some disadvantage in these circumstances. Perhaps they are slightly less efficient than Dacnini in exploiting nontubular flowers and/or catching small arthropods; their peculiarly shaped bills may be less than ideal for such activities. They might not be able to compensate for this inferiority by tapping the tubular flowers that do exist in the lowlands for any one or all of several reasons. Perhaps such flowers are not sufficiently abundant or are already preoccupied by insects or lowland hummingbirds. The extra effort of flower-piercing could also be particularly deleterious in the lowlands, where the fauna is richer in species than in the highlands, and niches may be more tightly packed or finely divided and many resources more scattered or patchy in distribution (see discussions in Pianka, 1966, and MacArthur, 1972).

Although hummingbirds probably are not often in direct or serious competition with honeycreepers now, given the existing arrangements, their presence in an area must limit the scope for ecological and evolutionary maneuvering by either diglossas or Dacnini. The abundance of hummingbirds in the mountains of Central America may have discouraged invasion of these highlands by dacnine honeycreepers, even though the local diglossas are comparatively scarce and little varied, by Andean standards.

The conebills have another characteristic mix of habits and techniques.

They are generalists in having simple short bills and taking many arthropods as well as nectar, but they also seem to be ''marginal'' (Moynihan, 1968b). Many of them, probably including all the Andean forms (except *Oreomanes?*), are commensals of man or of other birds. This is certainly true of the forms that are obligate or very frequent associates of mixed flocks. Some populations of *C. cinereum* seem to have become dependent upon man-made habitats. The same and other populations may extract nectar from holes made by diglossas. The absence of conebills from the mountains of Mexico could be related to the poverty of diglossas. There may be an old predilection for holes, a preadaptation to use them, in the conebill stock. Another member of the group, lowland *Coereba*, is known occasionally to cut holes in flowers with its only slightly elongated and curved bill (Borrero, 1965). This may be further evidence of a phylogenetic link between conebills and diglossas.

5

CONSIDERATION OF THE DIGLOSSA CLUSTER

The development of specialized social responses among individuals of different species is a refinement of competitive strategy, perhaps inevitable in many cases (see below) but not always easy to understand. It may be useful, therefore, to analyze, or at least comment upon, some aspects of the interspecific reactions of members of the diglossa cluster, their immediate and distant causes, motivations, functions, and probable courses of evolution.

IMMEDIATE CAUSAL FACTORS OF INTERSPECIFIC BEHAVIOR

The question of motivation is simple in some respects, difficult in others. There are three kinds of behavior to be considered.

It seems very probable that the internal tendencies of diglossas and of conebills, such as *C. cinereum,* that are engaged in open interspecific disputes are not *qualitatively* different from those of the same and related species during intraspecific disputes. As far as I could tell, all the actual movements of attack, escape, etc., used during fights between different species are identical in form with some of the patterns used in fights between individuals of the same species. But the various motor patterns certainly are not used with equal total or relative frequencies in the two types of social situations. Both the similarities and the differences are suggestive.

The fact that the patterns shown during intraspecific disputes are not distinctive would seem to indicate that these birds—when such disputes do occur—must regard, in some sense, all their antagonists as members of a single group or social unit. Presumably they regard individuals of certain other species as other members of their own species in some circumstances. The reverse, i.e., that all individuals of the same or different species are regarded as equally "foreign," is improbable. Intraspecific disputes occur in all birds and most other highly organized animals, while interspecific disputes are generally rarer and apparently confined to only some species and groups. Even among diglossas, of course, there are populations that do not show such behavior. On general comparative grounds, it is more likely that the habit of engaging in interspecific disputes evolved as an extrapolation of intraspecific hostility rather than vice versa.

If this is correct, then some aspects of the hostile behavior of the members of the diglossa cluster are similar to corresponding aspects of the friendly behavior of species in mixed flocks. Again see below.

If individuals of one species react to individuals of other species as if they were all members of the same broad social unit, friendly or unfriendly, then the sign stimuli by which members are recognized must be diverse. They must be considerably more varied than the usual run of species-specific stimuli. A *D. carbonaria* that reacts to *D. cyanea, C. cinereum, D. lafresnayii,* several hummingbirds, and possibly other species in some of the same ways is certainly catholic in its tastes. It is prepared to recognize as essentially equivalent to one another a whole range of colors and color patterns, movements, postures, and sounds. It must be either remarkably analytical or remarkably undiscriminating. It is, in fact, analytical.

Even when interspecific reactions are at their sloppiest and most frequently openly aggressive, as in the central and eastern cordilleras of Colombia, they do not extend indefinitely. They are restricted to a selection of species, wide or narrow; and the species selected are not only the ones that resemble the aggressors most closely.

There is another relevant point to be mentioned in this connection. Many of the interspecific attacks among members of the diglossa cluster of the Andes are in some sense ''personal,'' unlike the presumably simple defensive reactions of *Lampornis calolaema* or *L. castaneoventris* cited above. These personal attacks may be directed toward individuals that are not nesting or feeding or doing anything else very significant at the time. The attacks, are, in other words, released by some intrinsic (and undisguisable) qualities of the victims, not only by particular behavior patterns or evidence of overt competition at any given moment. They are truly social and almost irrepressible.

The morphological differences between intra- and interspecific fights are twofold. Intraspecific disputes are briefer on the average and include less display (often none at all). Displays usually are produced in circumstances of frustration and/or when incompatible tendencies are nearly in balance (see Baerends, 1975). It would seem, therefore, that interspecific disputes are more unequal than intraspecific ones. This is common sense. Different species always differ in size, weight, shape, and strength, as well as in fighting techniques and commitment to given resources. One of the antagonists in an interspecific dispute is bound to be at a disadvantage from the beginning.

Reciprocal inhibition of songs may also entail paying greater attention to a wider variety of stimuli, in this case sounds alone, or perhaps distinguishing more configurations of stimuli, the characteristic song patterns of several different species. Its evolution must, however, have been more complicated than that of interspecific fighting. As it works in the Andes, it presupposes the recognition of a new and separate class of *Kumpans* or ''acquaintances,'' i.e., the inhibitors. A performing individual involved in this nexus of relations must distinguish among members of its own species (who may interrupt, or who may even provoke interruptions), and ''accepted foreigners'' (whom it would be impolite or impolitic to interrupt), and just plain unimportant or socially irrelevant foreigners (who may be interrupted or not at will). The nature of the response may also pose difficulties. The repression of an act is as much a response as its performance. An individual may have to treat certain species as a special class of foreign acquaintances in some contexts, i.e., singing, while treating them as other members of the same species in other contexts, i.e., fighting. This may help to explain why reciprocal inhibition of songs tends to break down most frequently in regions such as the central and eastern cordilleras of Colombia where interspecific fighting is inclined to occur rather often. Ambivalence and dual roles are difficult to sustain.

Social segregation by mutual avoidance within the same areas may be more specialized but less problematical. It entails paying increased attention to more stimuli, and also recognition of the same three social classes, viz, conspecifics, accepted foreigners, and unimportant foreigners, but the class distinctions are fairly consistent or congruent. More often than not, a bird avoids the same individuals that it does not interrupt. The avoidance may have to be active. One species may have to retreat before another species, not merely refrain from advancing. But again, as in the case of interspecific fighting, the movements employed are not basically different in form from similar patterns used in some intraspecific encounters.

The recognition of new social classes is not, in itself, necessarily exceptional. Even the least gregarious species distinguishes among many categories, such as actual or potential mates, actual or potential rivals, real and presumed offspring (tolerated subordinates), etc. These categories cannot be completely stable. They must change, sometimes split or merge, *pari passu* with other modifications of behavior and ecology during evolution and with inevitable shifts of distributions and environments. The peculiarity or originality of the categories composed of foreigners lies in the diversity of the clues that must be identified and processed by the classifiers, the responding individuals.

Thus the evolution of the interspecific behavior of the members of the diglossa cluster of the Andes has been accompanied and accomplished by the development of increased sensitivity to a wider range of stimuli in several contexts, with some changes in frequency and timing and doubtless orientation of responses, but not the appearance of new kinds of responses. This may illustrate a general rule, typical of most interspecific relations of most animals. Specialized interspecific reactions do not usually involve a new output but rather a receptivity in the central nervous system of the receiver to new inputs and a new adaptive classification of them.

VARIATIONS AND CORRELATIONS WITHIN REGIONS

Members of the diglossa cluster do not always behave in exactly the same ways throughout a region. Some local differences in behavior can be correlated with obvious differences in habitats.

There are more contacts (face-to-face encounters, usually with overt hostility and probably overlaps of songs) between different species in areas of large and dense avian populations than in otherwise similar areas of small and sparse populations. The more individuals there are, the more likely they are to meet one another at any level of caution or dislike. Also there are more contacts between species in relatively open habitats (scattered trees and bushes) than in closed habitats (crowded vegetation). This may be a matter of small-scale topography. There are more alternative perches and hiding places in closed habitats than in open ones.

The situation is complicated by a latent contradiction. The two positive correlations are negatively correlated with one another. In many areas of scrub and forest, populations of honeycreepers tend to be larger in thick than in thin vegetation. The frequency of contacts between species must depend upon an intricate interplay of factors that are often difficult to reconcile.

Densities of foods and predators and parasites probably are also positively linked to densities of vegetation and honeycreepers in many areas. They are not, however, always inseparable. They are sometimes disassociated in artificial or aberrant habitats.

Contacts between species tend to be less frequent on the average in natural-looking vegetation of almost any density than in unmistakably man-made, and usually more recently created or re-created, gardens, hedges, and plantations. There could be several reasons for this contrast. The historical element might be invoked. Birds must need some period of time to adjust and stabilize their social relations in situations that are both new and distinctive. But the time does not necessarily have to be long, and present conditions are highly pertinent. Some gardens and plantations provide concentrations of food. Some are rather open. Many are poor in predators. Any of these features might favor social recklessness (see also the preceding comments on *D. baritula "sittoides,"* a common garden form).

VARIATIONS AND CORRELATIONS BETWEEN REGIONS

Whatever the causes of differences between areas within a single region, they apparently cannot be extrapolated to explain all the contrasts between regions. Each region has its peculiar range or mix of interspecific reactions extending over a variety of habitats and population levels. They may involve quality as well as quantity. They do not seem to be correlated with the same features in the same ways.

Thus, for instance, members of the diglossa cluster may show different interspecific behavior in approximately equally densely populated areas of different regions. Recall that I found dense clumps of birds in most of the major regions, including all three cordilleras of Colombia and central Ecuador. Similarly, members of the cluster may show different behavior in approximately equally sparsely inhabited areas of different regions. Populations seem to be comparatively small at many sites from the north to the south of the humid cold zone, e.g., in or around Sierra Nevada de Santa Marta, Medellín, Cutervo, Chachapoyas, Cuzco, and parts of northern Bolivia. Conversely, the birds of both sparsely and densely inhabited areas of the same region tend to show similar or identical social behavior, as in the central cordillera of Colombia where the population near Medellín is very much less dense than the one on Puracé.

Other ecological factors also fail to coincide with general behavioral trends, which imply similarity between north and south and a contrast between both and the center. There is closed as well as open vegetation in almost all regions. Areas of dense vegetation may be relatively most numerous in the north, and areas of sparse vegetation in the south, but the structural extremes are similar almost everywhere; the birds of open areas in northern Peru do not react in the same manner as the inhabitants of open areas in northern Bolivia, nor do the birds of closed areas in Puracé behave like the inhabitants of closed areas on Munchique. Many of the most recently created habitats, such as gardens, are concentrated in and around towns and cities, but substantial human settlements occur throughout the north, center, and south. Farms with associated hedges and plantations are also widely distributed on a large scale, with only local irregularities, and probably were at least as nearly ubiquitous in pre-Columbian times. Abundances of food and predators must conform to these parameters, directly or indirectly.

The available ecological data are incomplete. My observations were confined to a limited number of sites. It is not always possible to be very definite or precise about averages of conditions. Some regions must be slightly wetter, more densely populated, and/or have thicker vegetation than others.

It is conceivable that such average phenomena could be the crucial determinants of regional differences in behavior. This does not, however, seem to me to be very likely, at least for most of the relevant variations. The argument against the hypothesis is inferential and must rely upon several lines of evidence, none of which is very strong or convincing in itself but which may reinforce one another. It has already been suggested that areas of relatively thick vegetation are more numerous in the north than in the south. This is a difference in averages as well as in points. Density of vegetation probably is often, perhaps inevitably, directly and positively correlated with humidity and the density of populations of birds. If so, the latter should also conform to the general north-south gradient. Which is just what the behavior does *not* do. The same discrepancy appears when particular regions are compared. Thus, the reactions of the birds of such northern regions as the eastern and central cordilleras of Colombia, and those of some southern regions, such as central and southern Peru, are "intermediate." However, the northern regions are almost certainly more humid on the average, with all that the difference implies for densities of populations and vegetation, than are the southern ones. More conspicuously, the extremes of behavior shown by the birds of northern Bolivia and the southern part of the western cordillera of Colombia are similar, even though the northern region again is probably appreciably more humid on the average. It may also be significant that the behavioral differences between the birds of different ecological facies within a region are not really very profound, even when the areas are fairly large. The northern and southern ends of the central cordillera of Colombia come to mind once more. Finally, one should remember that there are sometimes differences in behavior between the birds of closely adjacent regions that cannot differ very much in either ecology or population density, in detail or on the average. This may be seen in central Ecuador and northern Peru west of the Marañón vs. northern Peru east of the Marañón.

Perhaps the most nearly probable example of an average effect is the increased prevalance of interspecific territoriality in the south. This might be ascribed to a combination of less humidity, more open vegetation, and reduced population density at more points in the south than in the north. Open patches should have favored interspecific contacts, and the sparsity of individuals may have permitted the contacts to be controlled, on occasion at many sites, by a relatively simple division of living space (see Orians and Willson, 1964, and also below).

It still appears to be necessary to look for further causes of other regional differences in behavior. They cannot be taxonomic. Different taxa may have similar reactions. Populations of the same taxon may have different reactions in different regions.

Another factor that might have been expected to influence social and interspecific behavior, but apparently does not do so to any great extent in the Andes, is the number of species present in any given region. The number of species in the diglossa cluster seems to be about the same in many parts of the humid cold zone, or varies without obvious large-scale trends over great distances. I am, of course, referring to areas of some appreciable size, not particular sites of a few hundreds or thousands of square meters. The numbers of species of other birds that might impinge upon the members of the cluster as helpers or competitors, i.e., many nectarivores, insectivores, and frugivores, may change more regularly, but only more or less smoothly from north to south. (See the discussion of mixed flocks.)

Having discarded or discounted so many hypotheses and conjectures, it would seem only logical to consider some of the possible effects or aftereffects of strictly geographical parameters. The various regions of the humid cold zone are of different sizes. Each occurs in a particular place in a complex spatial arrangement. Either or both aspects could be pertinent.

Spatial relations between regions may be less important for members of the diglossa cluster than for birds of mixed flocks. I did not find any evidence to indicate that the degree of geographical isolation is particularly significant for the diglossas or their associates in most regions. For example, the members of the cluster on the very isolated massif of Santa Marta seem to have intermediate and rather undistinguished social behavior. Nor did I detect any special modifications of behavior among diglossas at the frontiers of regions; this is another contrast with the birds of mixed flocks.

There is, however, a *rough correlation between interspecific behavior and the size of regions*. One of the areas in which microgeographical and ecological separation of species of diglossas is most extreme is Munchique. This is a small island and part of the western cordillera that is a series of small islands. The other region in which behavior reaches a similar extreme is northern Bolivia, where the humid cold zone is also small, relatively narrow, and only tenuously connected, at best, to other stretches of similar environment to the north. The opposite extreme of interspecific behavior among diglossas, i.e. social segregation, is characteristic of Ecuador and northwest Peru, both of which are part of the largest continuous block of the humid cold zone in the central Andes.

The regions of the northern Andes that have diglossas with intermediate behavior are also intermediate in size (even the mountains at the northern end of the western cordillera of Colombia are larger than Munchique). It seems probable that the semi-isolated stretches and peninsulas of the humid cold zone in southern and central Peru that have birds with intermediate behavior are also broader, on the whole, than the corresponding region of Bolivia. They certainly are smaller than the main central mass.

Why should this rough correlation exist? Many or all of the behavior patterns involved are hostile or agonistic, and doubtless concerned with competition. Even when purely hostile, competition can take different forms. It must be assumed that conditions favor different forms for members of the diglossa cluster according to regular geographic rules. Given the sorts of variation observed, it seems likely that the size of a population, which must accord with the size of an area inhabited, is the critical feature that has determined the direction and strength of selection and / or social pressure upon interspecific behavior in any given region.

Different kinds of hostility have different advantages and disadvantages. Fighting entails the risk of physical injury but offers a chance of decisive victory over an antagonist or rival within a limited period. The victor of a fight may hope to appropriate all the resources in dispute. Avoidance and other segregation patterns are less dangerous but more time-consuming and perhaps difficult to sustain. The participants in a system of segregation may have to share resources indefinitely. The relative advantages and disadvantages of the two kinds of interspecific behavior can hardly help but vary with the numbers of actual or potential rivals encountered or anticipated.

As previously noted, the microgeographical and ecological separation of members of the diglossa cluster in small regions probably is a result of fighting. Members of the cluster should often have been able to expell rivals of other species from particular sites and habitats within such regions at small cost, by a small number of fights, simply because the rivals were few. The birds of the large mass of the central Andes may not have had the same option. Birds that were aggressive toward other species would have had to fight a large and long series of antagonists, probably suffering unacceptable costs. In these circumstances, they probably have had to develop a degree of tolerance *faute de mieux.* Why they should not have become friendly to one another is a question that will be raised in the final discussion.

The argument may be illustrated by a hypothetical example. Consider one region with a population of 100 individuals of species A and 100 of species B, and a second region with a population of 1,000 individuals of species A and 1,000 of species B. At first glance it might be assumed that the effects of interspecific fighting would be similar in the two regions, as the ratio of A to B is 1 to 1 in both. This is not, however, likely to be the case. Many species of birds, and certainly most honeycreepers, finches, and other small passerines, tend to move into areas left vacant by other members of their species. Thus, in this example, an individual of species A in the first region will have to face, at worst, 100 antagonists of species B, while an individual of A in the second region might have to face 1,000 B's. Doubtless the situation is never quite so simple in nature, but the general trend is clear. In this kind of interspecific relationship the actual numbers of individuals of different species can be more significant than their relative numbers or the ratios between them.

It will be seen that I do not agree with the suggestion of Murray (1971) that interspecific aggression is always "misdirected." Such behavior can be advantageous on many occasions in many circumstances, and is often correctly directed with great precision.

Interspecific relations affect species diversity. Although the total numbers of species of the diglossa cluster in a region do not seem to vary appreciably, there are obvious differences between regions in average diversity at any given point. The average number of species of the cluster per point tends to be less in the far south and the far north where separation is extreme. It is greater in the center where segregation is nearly perfect. It is sometimes greater yet in intermediate regions characterized by partial separation, partial segregation, much flexibility of behavior, and many breakdowns of social rules.

Social relations in intermediate regions reflect intermediate locations. Only the variability of behavior is puzzling. Behavioral stereotypy is usually favored during evolution. It facilitates speed, clarity, and decisiveness of responses. All other things being equal, these qualities are better than hesitation or confusion. Thus, one might expect that the interspecific reactions of the birds of intermediate regions would have become stereotyped—at least more stereotyped than they seem to be now—while remaining intermediate in form(s). Perhaps the regulation of ambivalent and complicated reactions is a more difficult, and therefore lengthier, process than the stabilization of more extremes or consistent patterns. Perhaps the variability of behavior in the less completely isolated intermediate regions is maintained or frequently restored by the arrival of strays from other regions.

Several authors, e.g., Hamilton (1962), Johnson (1963), Murray (1971), and Orians and Willson (1964), have discussed probable or possible sequences of behavioral interactions when two closely related species, differentiated in isolation, come together and manage to coexist while competing to some significant extent. There has been an assumption, explicit or implicit, that overt hostility is usually the first interspecific arrangement to develop with or immediately after contact, and that it is often selected against later if the contact continues. The diglossa cluster sheds little light on the initial stages of contact. Most of the members of the cluster have been in most of the regions for a long time (long enough to have evolved local subspecies). What the arrangements among diglossas and their colleagues do suggest is that there is no general or inevitable sequence during later stages of contact and competition. On the present evidence there is no reason to suppose that microgeographical separation is more primitive than social segregation or vice versa. Each system is adapted to its own conditions.

The following pages will show that other systems also occur and appear to be equally functional, for some of the same and some different reasons, in the same areas.

6

SOME MIXED FLOCKS

COMPOSITION AND SCOPE

The second cluster to be considered in this study includes a host of species. Many of them are common, conspicuous, and dominant in some or all forest and scrub areas of the cold humid zone. They were observed in most of the same places as the diglossas described above, and at many of the same times.

The members of this second cluster belong to different genera, families, subfamilies, and even orders. The taxonomic categories do not, however, always coincide with behavioral or ecological ones. Based on observations in the field, most of the birds can be grouped as follows.

1. Brush-finches. There are many species of the genus *Atlapetes* and closely related forms. These are rather large finches, with bills of moderate size, strong legs, chunky bodies, and fairly long tails. The colors of some species have already been mentioned. There is a considerable range of patterns within the group as a whole, but all the forms are rather boldly marked with black, gray, white, yellow, olive, and/or chestnut. They are primarily terrestrial or spend most of their time low in vegetation, in dense scrub or understory, but can go high in trees on occasion. They eat a great variety of foods including seeds, berries, buds, and doubtless many small arthropods and other invertebrates that they pick up from the ground or glean from twigs and leaves.

2. Bush-tanagers and bush-warblers. Under this general heading can be included a great number of small- to medium-sized fruit- and insect-eating birds such as *Chlorospingus*, *Cnemoscopus*, *Hemispingus*, and *Basileuterus*. They tend to be less terrestrial than brush-finches (some are thoroughly arboreal), but are similar in color or tone, mostly olive above and yellowish below, usually with markings of brown, white, and/or blackish, especially around the head (see, also, Eisenmann, in Griscom and Sprunt, 1957, for further descriptions of some of the species). *Thlypopsis*, with orange on the head, may be related to this group. Black, gray, and white *Urothraupis stolzmanni* may be related to this group and/or to *Atlapetes*.

3. Bright tanagers. Many other tanager-like birds of the Andes are more vividly colored than those mentioned above. A large series of bright forms includes species of *Iridosornis*, *Anisognathus*, and *Buthraupis*, and possibly *Delothraupis castaneoventris*.[1] These birds are medium to large in size. They move through trees and scrub, seldom coming down to the ground, and feed on fruits, buds, other vegetable materials, and small arthropods. They all have substantial amounts of bright blue in the plumage, usually combined

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[1] I have taken the scientific names of the birds from de Schauensee, 1970, and Storer, 1970. The Storer classification of the tanagers is progressive, with much lumping. Other catalogues and accounts have recognized more genera, or given different names, e.g., *Poecilothraupis, Compsocoma, Tephrophilus,* to some of the same birds.

with black or olive on various parts of the body, and areas or patches of yellow, buff, chestnut, orange, or red below and/or on the head.

Two high altitude species of the genus *Thraupis, cyanocephala* and *bonariensis,* are also blue, yellow, olive, arboreal, and semi-omnivorous.

The so-called "Plush-capped Finch," *Catamblyrhynchus diadema,* appears in the field to be nothing more than another kind of *Iridosornis.*

The supposed tanager *Chlorornis riefferi* is grass green.

The enormous genus *Tangara* includes species of many different colors and patterns. They are all arboreal and rather small in size. Some of them may also be more insectivorous and less frugivorous than many of the larger tanagers. The genus has proliferated in the Andes, but mostly at low to moderate altitudes. Only a few species, such as blue and black *T. vassorii,* was seen frequently in the course of this study.

4. Whitestarts, *Myioborus.* As noted above (p. 28), these are small, arboreal warblers with flycatching habits, getting much of their prey by aerial sallies. They are blackish above, yellow below, with white edges to the tail. They also have rufous crown patches and/or white markings on the face.

5. Woodhewers, treerunners, spinetails, ovenbirds, etc. The colder parts of South America are inhabited by many species and genera of what may be called the family Furnariidae (see Feduccia, 1973, and review by Bock, 1974). They are small to medium sized, insectivorous, and dull colored in shades of brown and gray, but exceedingly varied in shape, structure, habitat preferences, and feeding techniques. Perhaps the most interesting species in the Andes are some treerunners and spinetails. Treerunners (like woodhewers) are reminiscent of woodpeckers or the treecreepers of the northern hemisphere. They spend much of their time moving up and down tree trunks and branches, probing for small arthropods in the bark. Spinetails are more similar to warblers or titmice. They tend to remain in scrub or understory and to feed by gleaning.

6, 7, and 8. Tyrannid flycatchers, true woodpeckers, and hummingbirds. These three groups are large and varied but often not directly relevant to the mixed flocks discussed here. The few species that will be considered are more or less conventional, for their groups, in appearance and some aspects of ecology. The tyrannids are small to medium, dull (olive, gray, brown), arboreal, and catch many insects in flight. The woodpeckers are brighter (black, red, green, sometimes with white or yellow), creep on trees, and feed by probing bark for small arthropods and drilling holes for grubs and/or sap. Some of them also take vegetable matter. The hummingbirds are largely iridescent green.

9. Conebills and diglossas. The conebills *C. sitticolor, C. rufum, C. ferrugineiventre,* and at least some of the white-capped populations of *C. albifrons* are certainly included in this cluster. So, to a lesser extent, are a few kinds of diglossas, most notably some populations of *D. cyanea.* Conebills of the blue-capped *C. albifrons "atrocyaneum"* type may also be incorporated into the cluster in several areas, although they often seem to prefer slightly lower altitudes than the forms cited above.

These birds are heterogeneous. What they have in common, i.e., why they can be assigned to the same social cluster, is the habit of associating with one another, at least in some places at some times. In most cases, where and when associations do occur, they are obviously "friendly." The friendliness seems to be real and specialized, the expression of a definite preference. It shows itself by following and joining. Some species follow and join others frequently. Some of the same and other species allow themselves to be followed and joined, or even encourage the process. The result can be the formation of mixed flocks.

The friendliness is not always unalloyed. There may be some hostility when different species get together. I noted threat calls and visual displays, alarm patterns, overt attack and escape movements, and intention movements. But such negative reactions are relatively rare among integral members of the cluster, and they may not interrupt associations more than momentarily.

The mixed flocks sometimes formed by these birds are not the only ones in the Andes. Almost every major habitat of the Andes has its characteristic associations. The groups in the *Polylepis* woods of central Peru have already been mentioned. Some habitats have several different kinds of associations. As far as I could tell, however, the flocks discussed here are the only well-developed and highly organized friendly assemblages in humid forest and scrub at high altitudes below the *Polylepis* level. They can include such a wide variety of birds that it is difficult to find an appropriately comprehensive name for them. They were called the "tanager cluster" in Moynihan (1973). I should prefer to call them simply "high altitude forest and scrub flocks" in the following pages whenever it is necessary or desirable to distinguish them from comparable associations.

The same species of birds, even the same individuals, can be members of more than one cluster simultaneously or in rapid succession in the same place or at adjacent sites. In the Andes this flexibility or duplicity is most conspicuous in some brush-finches and conebills and a few diglossas. It is not surprising. Different clusters are characterized by different kinds of interactions. An individual involved in two clusters has different correspondents, i.e., individuals to respond to, in each. Again it is evident that birds are capable of discriminating among, reacting appropriately and adaptively to, several different classes of *Kumpans*, friends, rivals, collaborators, etc., with a minimum of confusion, delay, or hesitation.

Different species play different social roles in mixed flocks. A general classification of such roles is offered in Moynihan (1962c). It is usually convenient to distinguish between "regular" and "occasional" members of flocks. It is also possible to recognize "nuclear" and "attendant" species by rough, practical criteria. A species can be considered nuclear if its behavior or appearance contributes appreciably to stimulate the formation, or to maintain the cohesion, of a flock. In some cases nuclear species can be classed as "active" or "passive." Passive nuclear species usually are joined and followed by other species much more frequently than they join or follow other species. Active nuclear species are the opposite; they usually join and follow other species much more frequently than they are joined and followed. The distinction is not, however, always clear-cut or exclusive or continuous. There may be exchanges, reversals, and combinations of roles. An individual, group, or species can be passive nuclear at some times and in some circumstances, and active nuclear at other times and in other circumstances. Some birds may even be active nuclear for some of their associates and passive nuclear for other associates, at one and the same time. As it happens, alternations and combinations of active and passive roles are particularly common in Andean high altitude forest and scrub flocks.

These Andean groups recall certain flocks of the Chiriquí highlands of western Panama (Moynihan, 1962c; Buskirk et al., 1972). At least one species and several genera occur in both associations, and there are other similarities in ecological types as well as in behavioral and spatial arrangements. Thus, for instance, the Chiricano groups, like those of the Andes, often include species that can be either active and/or passive nuclear, or move through different levels of vegetation from the tree tops to the ground. In both respects both montane associations differ from some lowland flocks, such as the mixed blue and green tanager and honeycreeper groups of central Panama in which there is less of a spread over different levels of vegetation and a greater distinction in social roles.

The joining and following patterns used in interspecific reactions are very similar to, or identical with, those used during many intraspecific encounters. This may be another indication that interspecific responses have been derived from intraspecific ones, primarily by a change in receptivity to new or previously irrelevant stimuli.

It is perhaps remarkable, therefore, that members of Andean groups can show extreme interspecific gregariousness without necessarily extending or elaborating their intraspecific relations to any unusual degree. With exceptions, which will be noted in the regional accounts, Andean flocks include only an individual, pairs, or small family groups of any given species at any given time, even when the sum total of members of different species is enormous. In this respect, most Andean groups differ from both highland and lowland associations of Central America. The latter usually include, and often seem to depend upon or to be formed around, larger groups of a single species, such as *Tangara inornata* or the local race of *Chlorospingus opthalmicus* (see also below) in Panama, and *Caryothraustes poliogaster, Chlorothraupis carmioli,* or *Tachyphonus delattrii* in Costa Rica (Slud, 1960).

In almost all mixed flocks it is evident that different species are obtaining different advantages from the associations. A single species of a mixed group may also be deriving multiple advantages, i.e., different benefits at the same or different times, from associations with the flock as a whole or interactions with particular components of the flock. The obvious advantages are food and safety. Individuals of different species may discover the location of food sources by watching one another (Krebs, 1973). Frugivores and nectar-feeders may even share the same items of food. Insectivorous birds, especially the flycatching types, may catch prey flushed by their companions. Some birds can learn new foraging techniques by observation and imitation (again, see Krebs, 1973). Members of flocks may also secure added protection. Extra eyes and ears may facilitate the detection of predators. The behavior of experienced birds should indicate danger spots to inexperienced ones. Mobbing by many birds of diverse aspects may distract predators more effectively than similar behavior by a few birds of less varied appearance and movement patterns. See, also, the recent review by Buskirk (1976).

There must be disadvantages as well as advantages to forming mixed flocks. Among the disadvantages may be increased conspicuousness to both rivals and predators and some intensification of competition at an immediate level. It will be argued below, however, that the usually moderate increase in competition should be less risky or deleterious in the long run, for many species, than some of the possible alternative arrangements.

REGIONAL SURVEY

Many aspects of the flocks in different regions may be summarized in lists, figures, and tables, with commentary. The accounts will be introduced by lists of regular or frequent members of the local flocks. The lists are incomplete. I must have missed some members of some mixed groups in many areas. The lists are also selective. Some species are not cited because their occurrences near flocks seemed to be coincidental or accidental. A few anomalous cases are reserved for separate discussion.

NORTHERN BOLIVIA

The members of the flocks of northern Bolivia included the following species:

Brush-finch: *Atlapetes rufinucha.*

Bush-tanagers and bush-warblers: *Basileuterus luteoviridis, Chlorospingus opthalmicus, Hemispingus atropileus, H. superciliaris, H. trifasciatus, Thlypopsis ruficeps;* probably also *Basileuterus signatus.*

Bright tanagers: *Anisognathus igniventris, Buthraupis montana, Catamblyrhynchus diadema, Delothraupis castaneoventris, Iridosornis jelskii, Thraupis cyanocephala.*

Honeycreepers: *Conirostrum cinereum, C. ferrugineiventre, C. sitticolor, Diglossa cyanea.*

Whitestart: *Myioborus melanocephalus.*

Furnariids: the spinetail *Cranioleuca albiceps,* the treerunner *Margarornis squamiger,* and several other unidentified species.

Tyrannids: *Mecocerculus* species (probably *leucophrys*), *Ochthoeca rufipectoralis,* a small rufous bird (probably *Pyrrhomyias cinnamomea*), and again several unidentified forms.

The unidentified species were rare, or only occasional attendants. This seems to have been true of almost all the forms that I failed to identify in flocks in other regions of the Andes as well (see below).

I did not notice any woodpeckers or hummingbirds in mixed flocks in Bolivia.

TABLE 1

Mixed Flocks above Unduavi, Northern Bolivia, October–November 1963

Hours of observation: 42 1/2
Average no. of individuals seen per hour: 8.94
Average no. of individuals seen in mixed flocks per hour: 5.41
Individuals seen in mixed flocks as % of total no. of individuals seen: 63.89%
Average no. of mixed flocks seen per hour: 0.94
Average no. of highly organized mixed flocks seen per hour: 0.61
Average no. of individuals per mixed flock: 5.75
Largest no. of individuals in one flock: 15
Average no. of species per mixed flock (based on 36 flocks in this case): 3.53
Largest no. of species in one flock: 8

Well-developed or definite flocks were seen only in the humid areas with thick vegetation in the *yungas.* The amount and frequency of interspecific gregariousness varies with habitat and season everywhere. Some dimensions of the variation in Bolivia are indicated in Tables 1–4, which summarize a few counts that were made above Unduavi, mostly along the path to Cillutinarca, in late 1963, when many individuals of many species were breeding; and also in early 1964, when breeding had declined. Included are counts made below Unduavi, mostly along the road to Coroico, during the same periods. The rainy season in La Paz is December–April.

These and the following tables are presented primarily for purposes of illustration. The data included in them are partial. Most counts were made at a late stage of my work in any given region, or of a period of work in a region, after I had watched the local birds for some considerable time and made qualitative assessments of their behavior. I continued general observations while counting. Thus, the discussions and analyses of flocks will rely at least as heavily upon qualitative information as upon quantitative data.

Some aspects or details of the tables may need further explanation. The "number of individuals seen" refers to "relevant" individuals, i.e., all forest and scrub finches, tanagers, honeycreepers, warblers, etc., that might be supposed to be capable of, and potentially interested in, associating with mixed flocks, irrespective of whether or not they actually did so at the particular time and place of the count. The limits of relevance in this sense are somewhat arbitrary, but I think that I used the same criteria in all regions. The "highly organized" flocks are the groups of greatest cohesion, those in which individuals stay close together, within a few inches or feet of nearest neighbor, more or less consistently, for at least a few minutes and usually longer. Such a flock tends to move steadily, often rapidly, along a roughly circular path over a wide area. It is possible, therefore, to meet the same group, or what is partly the same group, again and again in different places. I must have done so on many occasions. As a precaution, to reduce bias, I never counted an assemblage that might have been a continuation of one counted earlier except after a lapse of one-half hour or more. There is usually

TABLE 2

Mixed Flocks above Unduavi, Northern Bolivia, February–March 1964

Hours of observation: 23 1/2
Average no. of individuals seen per hour: 7.85
Average no. of individuals seen in mixed flocks per hour: 5.74
Individuals seen in mixed flocks as % of total no. of individuals seen: 73.52%
Average no. of mixed flocks seen per hour: 0.94
Average no. of highly organized mixed flocks seen per hour: 0.76
Average no. of individuals per mixed flock: 6.14
Largest no. of individuals in one flock: 20
Average no. of species per mixed flock: 3.91
Largest no. of species in one flock: 12

a change in the composition of a flock during an interval of such length.

This raises an important point. Phrases such as "number of individuals seen" and "number of mixed flocks seen" are really shorthand for the numbers of counted sightings of individuals and groups.

Other counts at other sites in Bolivia and at other times would have produced more or less different figures. It was evident, nevertheless, that the implications of Tables 1–4 are generally correct. The high altitude forest and scrub flocks of this region *are* relatively common, frequently cohesive, and comparatively large on the average.

Many of the social reactions and relations within them are quite typical. The proportion of species that can be active and/or passive nuclear is considerable. It is often difficult or impossible to distinguish regular leaders or followers at first glance. There is a great deal of "leap-frogging," one species passing ahead of another and then being passed in turn. Some groups give the impression of being all followers and no leaders. Obviously the impression cannot be correct. Closer inspection reveals a variety of differences among the social roles of at least the most abundant and conspicuous species.

Some forms certainly do tend to follow and join individuals of other species more frequently than they are followed or joined. The brightly colored *Catamblyrhynchus diadema* and *Iridosornis jelskii* seem to be primarily active nuclear. The less conspicuous *Margarornis squamiger* might be classified as a regular attendant.

Some species are even more continuously or frenetically active than others, or make frequent excursions around the peripheries of groups. Examples include *Myioborus melanocephalus, Mecocerculus,* and *Conirostrum sitticolor;* possibly, also, *C. ferrugineiventre,* when present. Such birds often appear to be in the forefront of a group. This does not necessarily mean that they are the real social leaders. They may guide a group only when and if they are followed or joined by other species of greater social "weight." The latter may or may not decide to do so. If they do, the remainder of the group accompanies them. If they do not, the ostensible "guides" usually turn around, come back, and go along with the others. Thus the guides, despite their appearance of being passive nuclear, probably are really (more

TABLE 3

Mixed Flocks below Unduavi, Northern Bolivia, October–November 1963

Hours of observation: 19 3/4
Average no. of individuals seen per hour: 7.90
Average no. of individuals seen in mixed flocks per hour: 1.87
Individuals seen in mixed flocks as % of total no. of individuals seen: 23.72%
Average no. of mixed flocks seen per hour: 0.51
Average no. of highly organized mixed flocks seen per hour: 0.05
Average no. of individuals per mixed flock: 3.70
Largest no. of individuals in one flock: 8
Average no. of species per mixed flock: 2.50
Largest no. of species in one flock: 5

often) active nuclear, although in a somewhat peculiar way.

Most of the species of greatest social weight are brush-finches and bush-tanagers, and bush-warblers. These are the birds that tend to stick to the dense vegetation of scrub or understory, seldom going very high into trees. *Atlapetes rufinucha* and *Hemispingus trifasciatus* may be the most "ponderous" species in the areas of northern Bolivia in which I worked. *Basileuterus luteoviridis, Hemispingus superciliaris,* and *Thlypopsis ruficeps* can be only slightly less important. The social cores of the great majority of mixed flocks, almost all the largest and most cohesive groups, include one or more of these species. They can be nuclear in different ways, in different associations with one another and with other birds, but they seem to be more often, or more significantly, passive than active. For most purposes it may be convenient to describe them simply as "core species."

Cranioleuca albiceps was seen less frequently, but appeared to be subserving the same functions.

Local *Conirostrum cinereum* may play a similar social role on a reduced scale. Near Unduavi these conebills associate rather closely with the bush and brush forms in second-growth and scrub, but they probably are less attractive, less effective as nuclei, because they are quieter, duller, and often rarer than the others.

Chlorospingus opthalmicus is certainly another core species. It differs from the brush-finches and some other bush-tanagers in preferring higher levels of vegetation, usually moving through trees and seldom coming down near the ground. The *C. opthalmicus* observed in Bolivia and elsewhere in the Andes differ from other populations of the species in western Panama in being less gregarious among themselves, apart from their associations with mixed flocks. At high altitudes in the Andes these tanagers usually occur as single individuals, pairs, or small family groups, like most of their associates. At somewhat lower altitudes in Chiriquí, groups of what seem to be several families are fairly common. Presumably not coincidentally, *C. opthalmicus* of Chiriquí is usually passive nuclear in mixed flocks, while individuals of the species in the Andes are characteristically more ambivalent, perhaps as often active as passive.

TABLE 4

Mixed Flocks below Unduavi, Northern Bolivia, February–March 1964

Hours of observation: 10 1/4
Average no. of individuals seen per hour: 10.34
Average no. of individuals seen in mixed flocks per hour: 6.44
Individuals seen in mixed flocks as % of total no. of individuals seen: 62.26%
Average no. of mixed flocks seen per hour: 1.17
Average no. of highly organized mixed flocks seen per hour: 0.78
Average no. of individuals per mixed flock: 5.50
Largest no. of individuals in one flock: 11
Average no. of species per mixed flock: 2.92
Largest no. of species in one flock: 5

Hemispingus atropileus resembles its congenors in many aspects of behavior, but it is largely confined to bamboo thickets. Mixed flocks sometimes enter and pass through such thickets. Individuals and groups of *H. atropileus* may be incorporated into the core. They probably join and follow less frequently than they are joined and followed. They tend to disappear from a group that leaves bamboo (see below). All or most individuals of *Catamblyrhynchus* also prefer bamboo, but they seem to be less nearly exclusively confined to it than is *H. atropileus* in Bolivia.

The arboreal, brightly colored, tanagers, *Anisognathus igniventris, Buthraupis montana,* and *Thraupis cyanocephala* are both restless and particularly wide-ranging. They tend to join and leave flocks with superficially erratic frequency. When they are with flocks they are obviously influential, and seem to be primarily passive nuclear, joined and followed more often than joining or following. They are not, however, always followed when they fly far away. Nor will they necessarily hurry to rejoin a group if they are not followed. Thus, they are more independent than such forms as *Myioborus melanocephalus* and *Conirostrum sitticolor*. They could also be classified as occasional nuclear species.

Some of these tanagers provide examples of a type of variation that is widespread in the Andes. *Thraupis cyanocephala* may associate with mixed flocks rather less frequently in northern Bolivia than in many other regions. Conversely, I saw more *Buthraupis montana* in flocks in Bolivia than anywhere else.

The local combination of species, roles, and habitat preferences has an inevitable consequence. Members of mixed flocks range from high in the tree tops down to the ground, but the most weighty core species in this region, and those that associate with flocks most frequently or consistently, are primarily birds of low vegetation. Thus, the mixed groups of northern Bolivia can be considered to be, in some cases, "anchored" to the bottom. The high-flying forms may range far afield, tilt or drift in one direction or another, make excursions or go off on their own, but the actual course of a group is usually determined by its lower or more skulking members.

One contributory factor is obvious. Mixed flocks are noisy. Noise helps to keep members of a flock together. It also helps to attract new members. The montane forest and scrub flocks of northern Bolivia are distinguished by a particular range of sounds: sharp call notes, longer and more plaintive "Zeee" notes, hard rattles, and rapid twittering phrases. It is the birds of relatively thick and low vegetation, e.g., *Atlapetes, Hemispingus,* and *Basileuterus,* that tend to utter such sounds most frequently or loudly.

They probably have a greater need to vocalize than their more arboreal associates, and can afford to do so at less risk. Simply because their preferred habitat is so dense, with such poor visibility, they must rely upon acoustic clues and signals to supplement visual input for the performance and coordination of many activities. Sounds may have a disadvantage in drawing the attention of predators, but the very thickness of the vegetation can be a partial protection, hiding the birds from sight or barring entry to such enemies as hawks.

The members of the high altitude forest and scrub flocks of the Andes are diverse in appearance. The larger Andean assemblages seldom have a single or simple color scheme. They are more variegated in color than are most associations of other areas and life zones. There is an interesting correlation among some patterns. In northern Bolivia at least, species that are primarily olive above and yellow below, e.g., *Hemispingus* and *Basileuterus,* tend more often to be followed than follow, while species that are blue or blue-gray above and chestnut or buffy below, e.g., *Catamblyrhynchus, Iridosornis jelskii,* and the more gregarious conebills, more often follow than are followed. Whatever their other functions, the two color schemes may also serve as "badges" or "liveries," visible indications of social attachments and propensities.

In the *yungas* mixed flocks are largest, most active, and noisiest when the weather is moderately bad, with much cloud or fog and drizzling rain.

The black and brown diglossas of the Unduavi area, *D. carbonaria brunneiventris* and *D. lafresnayii mystacalis,* occasionally occur in or near flocks, without interacting with the other members in a very close fashion. They sometimes appear to be rather wary of a group. It was my impression, in fact, that they are not gregarious in the same way as many other birds (see, also, above). They may be doing little more than trying to usher or escort a nuisance out of the neighborhood, just as they might escort a mildly irritating or alarming rival or potential predator.

Individuals of the local *Diglossa cyanea* population seem to be even more ambiguous. They may be hostile escorts in some circumstances or friendly joiners and followers in others.

Every well-developed or highly integrated mixed flock tends to have its own range, usually of several thousand square meters. The same group, or a group of similar composition, can be found in the same series of places day after day. There seems to be some occasional overlapping of the ranges of adjacent flocks, one group appearing at a site that is also visited by another, but usually only when the other is far away. I saw few or no mergers between well-formed groups. Nor did I see any fights between groups.

The various members of a mixed flock do not defend a joint territory.

Each component individual, pair, or family does, however, defend its particular territory against others of its own species. Most territories are smaller than group ranges, or overlap them only partially. The result is turnover. Birds usually associate with mixed flocks only on their own territories. When a flock crosses a territorial boundary, the owners of the territory being left by the group will drop out. This occurs even when the habitat is essentially continuous, not only when a group is going in or out of a distinctly different formation such as bamboo thicket. If the habitat is continuous, the dropouts may be immediately replaced by other birds of the same species whose territories are being entered. The species composition of a flock is more stable than its mix of individuals.

Flocks may assemble at any time of the day. In areas of high interspecific gregariousness, as in the *yungas*, most large flocks are formed or re-formed shortly after dawn and continue for hours. All flocks break up in the evening when the members scatter to different sleeping sites.

Mixed flocks are never all-inclusive or ubiquitous, although they may appear to be nearly so in some parts of the central and western cordilleras of Colombia. There are many species of birds of the humid cold zone of the Andes that are similar to members of the high altitude forest and scrub cluster in size, habitat preferences, and aspects of diets (taking insects and/or fruits and other plant materials), but which do not associate with mixed flocks, or do so only rarely or in a few areas. Among these unfriendly or exclusive types are most thrushes (Turdidae), most wrens (Troglodytidae), jays (*Cyanolyca*), some cotingas, e.g., widespread *Ampelion rubrocristatus*, and even other tanagers and finches, e.g., the saltators (*Saltator*) and certain kinds of *Atlapetes*. (The genus *Atlapetes* includes many species—see Paynter, 1978. As indicated above, many of the species are boldly marked with black, white, or yellow. These relatively conspicuous species may, for the purposes of this paper and in certain contexts, be referred to as *Atlapetes* "proper." Some of the "proper" forms impinge upon or enter the diglossa cluster and/or play important roles in mixed flocks. A few other species, that used to be placed in the genus *Buarremon*, are more soberly colored, even cryptic, and irrelevant to the diglossa cluster. Some species of this second group, such as *torquatus* and *brunneinucha*, are widely distributed in the lower reaches of the humid cold zone, or just below, but usually ignore, and are ignored by, members of the high altitude forest and scrub flocks when they happen to meet. A few exceptional interactions will be cited below.)

Most of the birds that are known to be unfriendly to other birds, or that are exclusive, were omitted from the counts.

It is easy to think of reasons why some species might avoid or be excluded from associations. Wrens, for instance, are inconspicuous when they are not vocalizing. They may be too obscure to be attractive. Many thrushes, on the other hand, are large, bold, brusque in movement. They may alarm of disperse other birds. Jays may be even more disruptive because they are occasionally predatory. It is still remarkable that so few of these birds, diverse as they are, have developed the interspecific gregariousness that is so characteristic of many of their relatives and competitors. Again it is clear that similar resources can be exploited by different methods.

There do not seem to be any mixed flocks like those of Unduavi in La Paz. Species such as *Conirostrum cinereum,* and the less friendly *Thraupis bonariensis* and *Saltator aurantiirostris,* are common in the city and its environs, but other forms such as *Atlapetes, Hemispingus,* and *Iridosornis* are rare or absent. Much of the vegetation in the gardens and parks of the city is as dense and lush as parts of the Unduavi area. However, as noted, this condition is probably recent, an effect of human activities, irrigation and the planting of exotics. The original vegetation must have been drier and more open. The local birds may reflect an earlier situation. Or perhaps the present gardens, rich as they appear to be, are as yet too small and scattered to support flocks or most flocking species.

SOUTHERN PERU

Species seen to be regular or frequent members of high altitude forest and scrub flocks.

Brush-finch: *Atlapetes schistaceus.*

Bush-tanagers and bush-warblers: *Basileuterus luteoviridis, Chlorospingus opthalmicus, Hemispingus superciliaris, Thlypopsis ruficeps.*

Bright tanagers: *Anisognathus igniventris, Catamblyrhynchus diadema, Delothraupis castaneoventris, Iridosornis rufivertex* (the Peruvian representative, *reinhardti,* is sometimes considered a separate species), *Tangara vassorii, Thraupis cyanocephala.*

Honeycreepers: *Conirostrum cinereum, C. sitticolor, Diglossa cyanea.* (Species that seem to be no more than "escorts" are omitted here and from the following lists.)

Whitestart: *Myioborus melanocephalus.*

Furnariids: *Margarornis squamiger, Pseudocolaptes boissoneautii, Synallaxis* sp.

Tyrannids: *Mecocerculus* sp. (probably *leucophrys*), *Ochthoeca* sp., *Pyrrhomyias cinnamomea,* and the rather contingid-shaped *Mionectes striaticollis.*

Other species will be cited below.

Mixed flocks of the forest and scrub type are very rare or absent from the vicinity of Cuzco, and even in the upper part of the Urubamba valley. These areas are relatively dry and open, somewhat like La Paz but with fewer gardens and parks. As would be expected, the situation is quite different in the more humid areas to the east. Tables 5–7 summarize some counts made at Machu Picchu in February 1964 and June 1966. Habitats and sites are grouped in two categories: the extremely wet summit and eastern and southeastern slopes, covered with natural-looking vegetation, and the more obviously disturbed and probably slightly less wet western and northwestern slopes. The rainiest season in the general area is supposed to be December–March, and the least rainy season April–August. Several species certainly

TABLE 5
Mixed Flocks at the Top and on the Eastern and Southeastern Slopes of Machu Picchu (most data from June 1966, a few counts from February 1964)

Hours of observation:	35
Average no. of individuals seen per hour:	9.43
Average no. of individuals seen in mixed flocks per hour:	7.83
Individuals seen in mixed flocks as % of total no. of individuals seen:	83.03%
Average no. of mixed flocks seen per hour:	0.97
Average no. of highly organized mixed flocks seen per hour:	0.63
Average no. of individuals per mixed flock:	8.06
Largest no. of individuals in one flock:	24
Average no. of species per mixed flock:	5.24
Largest no. of species in one flock:	20

were breeding in February of 1964. I saw less evidence of breeding in June of 1966.

The tables indicate that mixed flocks are as well-developed in Machu Picchu as at Unduavi, or perhaps even more so. The southern Peruvian flocks resemble the Bolivian ones in composition and activity. There are, however, differences in detail.

Thus, for instance, *Delothraupis castaneoventris* seems to be more abundant and important as a core species on Machu Picchu than at Unduavi. *Thlypopsis ruficeps*, on the other hand, may be less abundant. *Diglossa cyanea* is often conspicuously active nuclear in southern Peru. There also are apparent substitutions. *Iridosornis rufivertex* of Machu Picchu may replace and play the roles of *I. jelskii* of Unduavi.

The case of some *Atlapetes* has already been mentioned briefly. The reference may be expanded. *A. schistaceus* of Machu Picchu occupies the usual, very humid, niche of its type or group. This is the niche that, quite unusually, is occupied by *A. rufinucha* in northern Bolivia. Local *A. schistaceus*, like other members of the species in the northern Andes, is an influential component of the cores of flocks, probably more often joined and followed than joining or following, but active and reactive in many different relations and directions. The habitats preferred by *A. rufinucha* in the central and northern Andes are occupied on Machu Picchu by another species of similar appearance, *A. tricolor*. This species show little or no interspecific gregariousness. I rarely saw it near flocks. My impression was that its presence was accidental. The aloofness of *A. tricolor* is surprising, as it is a member of the *Atlapetes* proper section of the genus. *Atlapetes brunneinucha* also occurs on Machu Picchu and tends to ignore or keep away from flocks. This is not surprising. The species is a "*Buarremon*." *A. brunneinucha* of southern Peru is conventional.

The local flocks incorporate a particularly miscellaneous selection of birds of other types. *Mionectes striaticollis* may be a regular attendant. The large grosbeak *Pheucticus aureoventris* was seen in or near flocks several times. A male *Trogon personatus* and a pair of *Piranga flava* ("tanagers" that may

TABLE 6
Mixed Flocks on the Western and Northwestern Slopes of Machu Picchu, February 1964

Hours of observation: 27 1/2
Average no. of individuals seen per hour: 3.13
Average no. of individuals seen in mixed flocks per hour: 0.73
Individuals seen in mixed flocks as % of total of individuals seen: 23.26%
Average no. of mixed flocks seen per hour: 0.22
Average no. of highly organized mixed flocks seen per hour: 0.11
Average no. of individuals seen per mixed flock: 3.33
Largest no. of individuals in one flock: 4
Average no. of species per mixed flock: 2.50
Largest no. of species in one flock: 4

be quite closely related to *Pheucticus*) were each seen with a flock once. Even some wrens may be attracted. Machu Picchu is one of the few places in the high Andes where wrens were found with flocks on more than a very few occasions. Two species are involved, common and widespread *Troglodytes aedon,* and another, probably *Cinnycerthia peruana.* They are sometimes close to the core species near the ground, but I doubt that they are significantly nuclear themselves.

Some groups may include, or be accompanied by, gallinaceous birds of either one or two species, the wood-quail *Odontophorus balliviani* and the guan *Penelope montagnii.* Perhaps such associations would be commoner in other parts of the Andes if gallinaceous birds were not hunted so intensively, decimated and made shy almost everywhere.

Machu Picchu rises steeply from the Urubamba. There is continuous forest and scrub along some slopes from the banks of the river, ca. 1,900 m, up to the top of the mountain. It is easy for birds to stray from one habitat or life zone to another. I did, in fact, see many individuals wandering above the usually preferred altitudinal ranges of their species. Some probable examples, e.g., the trogon and the quail, have already been mentioned. There were others such as a few *Basileuterus coronatus*, *Tangara xanthocephala,* and *Myioborus miniatus.* They appeared to play much the same roles in

TABLE 7
Mixed Flocks on the Western and Northwestern Slopes of Machu Picchu, June 1966

Hours of observation: 21
Average no. of individuals seen per hour: 4.38
Average no. of individuals seen in mixed flocks per hour: 1.90
Individuals seen in mixed flocks as % of total no. of individuals seen: 41.30%
Average no. of mixed flocks seen per hour: 0.29
Average no. of highly organized mixed flocks seen per hour: 0.10
Average no. of individuals seen per mixed flock: 6.33
Largest no. of individuals in one flock: 8
Average no. of species per mixed flock: 4.17
Largest no. of species in one flock: 6

flocks as their resident congeners. Several individuals of the Blue-capped conebill *C. albifrons "atrocyaneum"* were active and ostensibly guiding in the tree tops, rather like *C. sitticolor*, but they tended to stay closer to *Diglossa cyanea* to whom they were clearly subordinate.

Mixed flocks seemed to be very slightly larger and perhaps more highly integrated, on the average, in areas where strays occurred than where they were absent. The correlation is suggestive (see the account of central Ecuador and the discussion on pp. 144–145).

CENTRAL PERU

Species seen to be regular or frequent members of high altitude forest and scrub flocks.

Brush-finch: *Atlapetes schistaceus.**[1]

Bush-tanagers and bush-warblers: *Chlorospingus* sp. (probably *canigularis*), *Hemispingus atropileus, H. frontalis, H. rubrirostris, H. superciliaris, H. xanthopthalmicus, Thlypopis ornata, T. pectoralis.*** Possibly also *Basileuterus luteoviridis* and/or *B. nigrocristatus*. The latter species are so similar to one another, and to *Hemispingus frontalis*, that they are difficult to identify securely in the field. I think that I saw more than one species of this general visual *Gestalt* in the flocks of central Peru.

Bright tanagers: *Anisognathus igniventris,*** *A. lacrymosus, Buthraupis eximia, Catamblyrhynchus diadema, Chlorornis riefferii, Delothraupis castaneoventris, Dubusia taeniata, Iridosornis rufivertex, Thraupis cyanocephala.**

Honeycreepers: *Conirostrum cinereum, C. sitticolor, Diglossa cyanea.* Also *Conirostrum albifrons "atrocyaneum"* (presumably a stray from lower altitudes here as on Machu Picchu).

Whitestart: *Myioborus melanocephalus.**

Furnariids: *Margarornis squamiger, Pseudocolaptes boisseaunotii*, the spinetails *Schizoeca palbebralis* and *Synallaxis unirufa*, and several others.

Tyrannids: *Myiarchus* sp., *Myiophobus ochraceiventris, Ochthoeca* sp., *Pyrrhomyias cinnamonea*, and *Uromyias* sp., almost certainly *agraphia* (de Schauensee, 1970, says that the species is known only from Idma above the Urubamba near Cuzco, but it might well be expected to occur farther north in similar environments).

Others: Several nondescript warblers (perhaps migrants from North America), an unidentified vireo, the cotinga *Pachyrhamphus versicolor*, the woodpeckers *Piculus rivolii* and *Veniliornis* (*passerinii?*), and 2–4 kinds of hummingbirds, including *Coeligena torquata*.

The timing of the seasons varies from year to year in this region. The heaviest rains usually begin in December and last for 3 or 4 months. They were weak and late in 1964. Many birds were just beginning to breed in

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[1] Species marked with a single asterisk were found in flocks at both Carpish and Panao; those marked with a double asterisk were found in flocks only at Panao; the remainder, the majority, were found in flocks only at Carpish. Some of the same species were also found elsewhere apart from flocks (see below).

TABLE 8
Mixed Flocks at Carpish Pass, May 1966

Hours of observation: 25
Average no. of individuals seen per hour: 13.00
Average no. of individuals seen in mixed flocks per hour: 9.44
Individuals seen in mixed flocks as % of total no. of individuals seen: 72.62%
Average no. of mixed flocks seen per hour: 1.04
Average no. of highly organized mixed flocks seen per hour: 0.64
Average no. of individuals seen per mixed flock: 9.08
Largest no. of individuals in one flock: 25
Average no. of species per mixed flock: 5.44
Largest no. of species in one flock: 17

February of that year; many were in full breeding condition in April 1963; there were fledged young in May 1966.

Tables 8 and 9 are counts of flocks near Carpish (both sides of the pass) and above Panao in May of 1966. Table 10 is a count of potentially ''flock-able'' birds around and above Palca in February of 1964.

Mixed groups are common and often large and cohesive at Carpish. Interspecific gregariousness is on the same scale as in the *yungas* of Bolivia. The roles of many of the local birds are similar to those of their relatives to the south. Other species not found or identified in the south may be important at Carpish. *Hemispingus xanthopthalmicus* is a core and nuclear species, ranging through many levels of vegetation, more often joined and followed than joining or following. *Anisognathus lacrymosus* is another core species. It seems to be more attached to mixed flocks in this area and less likely to drift away or to be separated than is *A. igniventris*. It is another ambivalent form, passive and/or active nuclear according to circumstances. *Coeligena torquata* is a conspicuous but probably only occasional attendant. The woodpeckers may be regular attendants. The spinetails are often in groups, presumably large families, in close association with core species, sometimes before and sometimes behind. They are strange, busy little creatures. They give the impression of being occupied with their own affairs.

TABLE 9
Mixed Flocks near Panao, May 1966

Hours of observation: 10
Average no. of individuals seen per hour: 6.40
Average no. of individuals seen in mixed flocks per hour: 1.50
Individuals seen in mixed flocks as % of total no. of individuals seen: 23.44%
Average no. of mixed flocks seen per hour: 0.40
Average no. of highly organized mixed flocks seen per hour: 0.10
Average no. of individuals seen per mixed flock: 3.75
Largest no. of individuals in one flock: 7
Average no. of species per mixed flock: 2.75
Largest no. of species in one flock: 4

TABLE 10
Birds of the Palca Area, February 1964

Hours of observation: 17 1/2
Average no. of individuals seen per hour: 4.51
Average no. of individuals seen in flocks per hour: 0

They can appear aloof while still following and joining, being joined and followed, frequently and regularly.

A few widespread species or superspecies, such as *Hemispingus superciliaris*, *Atlapetes schistaceus*, and *Margarornis squamiger*, may not be so common or so consistently associated with mixed flocks at Carpish as in some other regions. The relatively slight importance of brush and bush forms of low vegetation, in conjunction with the variety of bright arboreal tanagers and the abundance of *Hemispingus xanthopthalmicus*, makes for an even distribution of social weight. Mixed flocks of the Carpish area seem to be less dependent upon their lower members than are groups of northern Bolivia.

Carpish groups probably also tend to be larger and more active during fine weather than in rain or fog.

I did not see high altitude forest and scrub flocks in the immediate vicinity of Tarma. The local habitats are all too reminiscent of Cuzco.

There are flocks above Panao. They are rare, small, brief, and loose. I did not encounter any relevent groups around or above Palca while compiling Table 10; but my earlier observations suggested that fugitive and transitory associations, rather like those of Panao, may occur here on occasion. Obviously, different parts of the region are characterized by different indices of interspecific gregariousness. The poor development of mixed flocking near Panao and Palca is noteworthy for several reasons. The vegetation and bird fauna of these areas are less rich than those of Carpish, but neither is really depauperate. Even at Palca I saw *Atlapetes schistaceus*, *Basileuterus* and/or *Hemispingus* spp., *Thlypopsis pectoralis*, *Conirostrum cinereum*, *Anisognathus igniventris*, and many flycatchers and furnariids. They were all remarkably nonsocial. There would have been more and better flocks in similar environments in either southern Peru or northern Bolivia (e.g., along the road to Coroico). All this would suggest that central Peru is a transitional region for mixed flocks, as well as for the diglossa cluster. It may foreshadow the central Andes, i.e., central Ecuador, in this respect as in others.

Northern Peru

There are further variations and contrasts here, but the region may still be considered as a whole for purposes of subsequent discussions of interspecific gregariousness.

Species seen to be regular or frequent members of high altitude forest and scrub flocks.

TABLE 11
Mixed Flocks near Chachapoyas, February 1964

Hours of observation: 13
Average no. of individuals seen per hour: 5.38
Average no. of individuals seen in mixed flocks per hour: 0.69
Individuals seen in mixed flocks as % of total no. of individuals seen: 12.86%
Average no. of mixed flocks seen per hour: 0.23
Average no. of highly organized mixed flocks seen per hour: 0
Average no. of individuals seen per mixed flock: 3
Largest no. of individuals in one flock: 5
Average no. of species per mixed flock: 2.33
Largest no. of species in one flock: 3

Brush-finches: *Atlapetes rufinucha, A. schistaceus.**[1]

Bush-tanagers and bush-warblers: *Basileuterus nigrocristatus.** Possibly also *B. luteoviridis, Hemispingus frontalis,* and *Thlypopsis ornata.**

Bright tanagers: *Anisognathus igniventris,*** *A. lacrymosus,** *Tangara vassorii,** *Thraupis bonariensis, T. cyanocephala.*

Honeycreepers: *Diglossa cyanea*?*

Tyrannids: *Mecocerculus* sp.,* possibly *stictopterus.*

Others: The peppershrike (vireonid) *Cyclarhis gujanensis,** and the woodpecker *Veniliornis* sp.,* probably *fumigatus.*

The general sequence of seasons must be much the same as in central Peru. I was told that at Chachapoyas April is usually the wettest month and August the driest. The year 1964 seemed to have begun normally here. The local honeycreepers and some of the tanagers were in full breeding (courting) condition at the time of my visit in February. There were also fledged young of several species, still being fed by their parents, near Cutervo in June of 1966.

Table 11 is a count of flocks on Tinaja above Chachapoyas in February 1964. Table 12 is a count of flocks in second-growth vegetation in the environs of Cutervo in June 1966.

The avifaunas of these areas are comparatively poor in species and individuals. The rarity of whitestarts (see above, p. 58) is particularly notable.

Other minor peculiarities of the region may be the direct consequences of poverty. Thus, for instance, *Thraupis bonariensis* occasionally occurs in mixed flocks here, something that it does not usually do elsewhere. It may develop a special link to *T. cyanocephala.* Both species are less common than usual here. Individuals of either one or both may become so deprived of companionship that they have to put up with second best. I also saw several attacks by *Aglaeactis cupripennis* upon very different birds, *Thraupis cyanocephala* and *Veniliornis* sp., near Cutervo. They could have been more

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[1] Species marked with one asterisk were seen in mixed flocks only near Cutervo; those marked with two asterisks were seen in mixed flocks only near Chachapoyas; the others were seen in flocks in both areas (comments below).

TABLE 12
Mixed Flocks near Cutervo, June 1966

Hours of observation: 17
Average no. of individuals seen per hour: 6.41
Average no. of individuals seen in mixed flocks per hour: 3.94
Individuals seen in mixed flocks as % of total no. of individuals seen: 61.47%
Average no. of mixed flocks seen per hour: 0.76
Average no. of highly organized mixed flocks seen per hour: 0.47
Average no. of individuals seen per mixed flock: 5.15
Largest no. of individuals in one flock: 13
Average no. of species per mixed flock: 3.62
Largest no. of species in one flock: 8

''overflow.'' In the absence of sufficiently large numbers of normal rivals, i.e., other members of the species and other nectarivores, *A. cupripennis* may have had to discharge its accumulated hostility (and this is one of the most bad-tempered of hummingbirds) upon inadequate or inappropriate objects.

''Escorting'' is fairly common in the region. As far as I could tell, however, *Conirostrum cinereum* does not join flocks in any friendly manner. Nor does *Diglossa cyanea* except, possibly and dubiously, near Cutervo.

The large scale ecological relations between the two widespread species of *Anisognathus* are puzzling. *Anisognathus lacrymosus,* like *Atlapetes schistaceus,* occurs in very humid areas in most parts of the Andes, while *Anisognathus igniventris,* like *Atlapetes rufinucha,* usually prefers slightly drier habitats. I do not know why *A. lacrymosus* is found near Cutervo. The Cutervo area does not, at first glance, appear to be more humid than Tinaja. It is quite the reverse, in fact. The combination of *A. lacrymosus* and *A. rufinucha* near Cutervo presents a piquant contrast with the combination of *A. igniventris* and *A. schistaceus* near Palca.

Mixed flocks are poorly developed at Tinaja. They are smaller and scarcer than might have been predicted by extrapolation from the southern Andes. The vegetation of the area is obviously disturbed but still moderately lush, as is indicated by the presence of *Diglossa coerulescens* and *D. lafresnayii unicincta.* More significant are three other species, *Basileuterus nigrocristatus, Hemispingus superciliaris,* and *Tangara vassorii.* They associate with mixed flocks in many other places. They certainly occur on Tinaja, but apparently without associating. Interspecific gregariousness would seem to be at least as depressed here as at Panao.

It can be even more depressed at other sites. I also worked along a ridge (not previously mentioned and name unknown) north of the Marañón Valley for several days. This area is 300–400 m higher than that at which the count recorded in Table 12 was made. It is farther away from the town of Cutervo and more nearly natural looking. In superficial appearance it is a simplified version of the slopes below the páramo of Guasca in the eastern cordillera of Colombia. Guasca has many birds and flocks, but at the time of my visit this Peruvian ridge was very impoverished in both individuals and species, and without any mixed groups at all.

The count areas near Cutervo are quite different. The local flocks are well-developed, possibly larger and more numerous than is normal or average for the region, although not for the southern Andes. This might be partly due to the fact that these areas are near an ecological boundary (see below).

Both near Cutervo and on Tinaja mixed groups are more active and conspicuous, and probably larger and more cohesive, in good weather than in rain or fog.

With all its variations, the region of northern Peru does seem to continue the transition to central Ecuador. The observed differences are interesting because they suggest that the transition is very uneven, with breaks and minor reversals, a variegated mosaic rather than a smooth cline. There may be an underlying patchiness of flocking through the humid cold zone as a whole, but it is often obscured by other trends and patterns. It is seldom as immediately visible to the naked eye as in northern Peru.

Central Ecuador

This is the region I visited most frequently and over the longest span of years.

Species seen to be regular or frequent members of high altitude forest and scrub flocks.

Brush-finches: *Atlapetes pallidinucha, A. rufinucha, A. leucopterus, A. schistaceus.*

Bush-tanagers and bush-warblers: *Basileuterus nigrocristatus, Hemispingus atropileus, H. superciliaris, Urothraupis stolzmanni.* Also *Basileuterus luteoviridis* and/or *Hemispingus frontalis;* and *Basileuterus coronatus* in one particular place.

Bright tanagers: *Anisognathus flavinuchus* (in the same place), *A. igniventris, A. lacrymosus, Buthraupis montana, Catamblyrhynchus diadema, Chlorornis riefferii, Dubusia taeniata, Iridosornis rufivertex, Tangara vassorii, Thraupis cyanocephala.*

Honeycreepers: *Conirostrum cinereum, C. sitticolor, Diglossa cyanea.*

Whitestart: *Myioborus melanocephalus.*

Furnariids: *Margarornis squamiger, Psuedocolaptes boissoneautii, Synallaxis unirufa,* other *Synallaxis* spp., probably including *azarae.*

Tyrannids: *Mecocerculus* spp., probably both *leucopterus* and *stictopterus, Uromyias agilis.* Possibly *Pyrrhomyias cinnamomea, Contopus* sp., and more obscure forms.

Others: The migrant North America warbler *Dendroica fusca,* the cotinga *Pachyrhamphus versicolor,* and a woodpecker *Veniliornis* (*passerinii?*). Also the very large woodpecker *Phloeocastes pollens,* and the hummingbird *Coeligena torquata.*

As usual, different areas are characterized by more or less different social and ecological arrangements. In this region it is convenient to distinguish

TABLE 13

Central Ecuador; All Areas Apparently Suitable for Flocks, 1964 and 1966

Hours of observation: 111
Average no. of individuals seen per hour: 11.96
Average no. of individuals seen in mixed flocks per hour: 4.35
Individuals seen in mixed flocks as % of total no. of individuals seen: 36.37%
Average no. of mixed flocks seen per hour: 0.80
Average no. of highly organized mixed flocks seen per hour: 0.31
Average no. of individuals seen per mixed flock: 5.43
Largest no. of individuals in one flock: 17
Average no. of species per mixed flock: 3.38
Largest no. of species in one flock: 10

among three series of sites: (1) the "real" center, i.e., the plateau or shallow basin around Quito, plus the eastern slopes of the western border mountains and the western slopes of the eastern border mountains; (2) the western slopes of the western mountains (below San Juan, along the old road to Santo Domingo); and (3) the eastern slopes of the eastern mountains (Papallacta, etc.).

Various counts in some of these areas are summarized in Tables 13–17. They were made in January 1964 and March 1966. January is the beginning of the breeding season for many birds of cold humid habitats in this region; there are many young out of the nest by March.

Interspecific gregariousness among members of the high altitude forest and scrub cluster is minimal in the real center. As in Peru and Bolivia, mixed flocks of these birds are absent from semiarid environments and city gardens. More remarkably, they are also absent, or are very rare, over wide stretches of obviously humid and more natural-looking scrub and small forest (e.g., near Nono and above San Juan on Atacazo), in spite of the fact that these areas are inhabited by such forms as *Atlapetes rufinucha, Basileuterus* and *Hemispingus* spp., *Anisognathus igniventris, Dubusia taeniata, Thraupis cyanocephala,* and *Myioborus melanocephalus.*

It should be stressed that the vegetation of Nono and similar sites appears to be as dense and diverse as that of some other areas and regions in which mixed flocks are common, and that the poor development of gregariousness in the real center seems to be "intrinsic." Certain forms, especially *Atlapetes rufinucha, Basileuterus nigrocristatus,* and *Myioborus melanocephalus,* are obviously more socially detached in the center than elsewhere.

Table 15 is a count of birds and reactions in parts of the center, but it gives a somewhat misleading impression of conditions in the area as a whole. It includes observations from "atypical," transitional sites, not far from the eastern and western areas, as well as from typical ones at the center of the center. In fact, there are rather more from the former than from the latter. Interspecific gregariousness is better developed, or less suppressed or underdeveloped, at transitional sites than at the more numerous typical ones. Even so, no highly integrated mixed flocks were seen anywhere

TABLE 14

Central Ecuador; Areas in which Highly Organized Flocks Were Seen, 1964 and 1966

Hours of observation: 62 3/4
Average no. of individuals seen per hour: 14.49
Average no. of individuals seen in mixed flocks per hour: 6.96
Individuals seen in mixed flocks as % of total no. of individuals seen: 48.07%
Average no. of mixed flocks seen per hour: 1.16
Average no. of highly organized mixed flocks seen per hour: 0.54
Average no. of individuals seen per mixed flock: 5.99
Largest no. of individuals in one flock: 17
Average no. of species per flock: 3.66
Largest no. of species in one flock: 10

in the center; and the index of gregariousness, i.e., the proportion of individuals seen in mixed flocks of any kind, is comparatively low in Table 15. It would have been lower still had I concentrated on, or confined myself to, typical places and conditions. I think that I would probably have found indices of 0 in several areas in earlier years, but there seemed to be little point to recording absences of reactions or null behavior at the time. In retrospect I regret my impatience and obtuseness.

Other observations suggest that the scarcity of mixed flocks in the center is accompanied, and perhaps maintained, by interspecific hostility. I saw in the area of its outskirts many overt attacks and fights within the briefly formed, small and loose groups. Among the species seen to be aggressive were *Atlapetes rufinucha, Anisognathus igniventris,* and *Diglossa cyanea.*

The proliferation of fighting and attacks is not accompanied by a corresponding increase in the lower intensity, or more ambivalent, habit of escorting. As implied by the figures, escorting is very rare in the real center. Almost everywhere there seems to be a negative correlation between the size of mixed flocks and the frequency of escorting. Some of the reasons why are self-evident and trivial, but one may deserve to be mentioned. Escorting seems to speed a flock on its way; escorters want to be rid of intruders. But the mere presence of an escorter in full view may also, by adding to the variety and apparent size of a group, add to the attractiveness of the group for other forms. The disadvantage probably is minor in regions in which mixed flocks tend to be large anyway. It must become relatively greater as the average size of groups decreases.

The eastern and western areas, i.e., the outer slopes of the outer mountains, seem to be more humid on the average than the center. They have retained more and larger patches of dense, tall, natural-looking vegetation. There is impressive montane forest in some places. Consequently(?), these regions are inhabited by more species and individual birds.

It is perhaps not surprising that the eastern and western birds also show more interspecific gregariousness than do the inhabitants of the center. At a rough glance, gregariousness is comparable on both sets of slopes. Observations of the birds of both slopes are lumped together in Table 14. The figures

TABLE 15

Central Ecuador; Apparently Suitable Areas in which Highly Organized Flocks Were *Not* Seen, 1964 and 1966

Hours of observation: 48 1/4
Average no. of individuals seen per hour: 8.69
Average no. of individuals seen in mixed flocks per hour: 0.95
Individuals seen in mixed flocks as % of total no. of individuals seen: 12.33%
Average no. of mixed flocks seen per hour: 0.33
Average no. of highly organized mixed flocks seen per hour: 0
Average no. of individuals seen per mixed flock: 2.88
Largest no. of individuals in one flock: 4
Average no. of species per flock: 2.13
Largest no. of species in one flock: 3

show that mixed flocking in these areas, although high for Ecuador, is still lower than in the most favored areas of Bolivia or southern Peru with similar climates and vegetation. Obviously gregariousness is less developed, ranging from nonexistent to only moderate, in central Ecuador as a whole than in more southern regions. The social behavior of the members of the high altitude forest and scrub cluster of central Ecuador, and presumably the central Andes in general, is just as extreme as is that of their neighbors of the diglossa cluster, even though the extremism is expressed in a different way.

Many species are common to both the eastern and western slopes of Ecuador, and to some of the environs of Quito as well. I did, however, see a few species only on one set of slopes or the other. Thus, for instance, I found *Anisognathus lacrymosus, Atlapetes pallidinucha,* and *Atlapetes schistaceus* only in the eastern area, and *Hemispingus atropileus, Buthraupis montana, Catamblyrhynchus diadema, Chlorornis riefferii, Iridosornis rufivertex, Uromyias agilis, Synallaxis* spp., and *Coeligena torquata,* only in the west. Some of the apparent differences may be "accidental," due to mere chance in the course of counting (and I spent more time in the west than in the east), but others must be real.

When with flocks, the various species play the roles that would be expected of them, i.e., they behave in much the same ways as other representatives of the same or closely related species elsewhere in the Andes, granted the inevitable correlates of reduced frequency of group formation, smaller average group size, and more overt hostility. *Myioborus melanocephalus* goes on excursions and can appear to be a guide; the *Hemispingus* spp. are often passive nuclear; *Buthraupis montana* is nuclear but occasional; etc.

The medium-sized woodpecker *Veniliornis* sp. is a follower and joiner, a regular or occasional attendant. In this respect it probably is typical of most of its relatives that associate with mixed flocks in the Andes.

Guans were still fairly abundant in parts of the western area when I made my counts. They were very shy. I did not see them with flocks as in southern Peru, possibly simply because they were too frightened of me.

The migrant *Dendroica fusca,* the Blackburnian Warbler, seems to be

TABLE 16

Mixed Flocks Along Road to Santo Domingo, ca. 2,957–2,835 m, March 1966

Hours of observation: 14
Average no. of individuals seen per hour: 17.21
Average no. of individuals seen in mixed flocks per hour: 8.86
Individuals seen in mixed flocks as % of total no. of individuals seen: 51.45%
Average no. of mixed flocks seen per hour: 1.50
Average no. of highly organized mixed flocks seen per hour: 0.64
Average no. of individuals seen per mixed flock: 5.90
Largest no. of individuals in one flock: 15
Average no. of species per mixed flock: 3.67
Largest no. of species in one flock: 10

something between a regular attendant and an active if only mildly nuclear species. Blackburnians certainly join and follow other birds more often than they are joined or followed. They are often on the outskirts of groups and may appear to have little social weight. Yet the adult males in nuptial plumage, usually assumed before the spring migration, are rather brightly colored. They can hardly fail to add to the conspicuousness, and therefore presumably attractiveness, of the groups with which they are associated. Social factors may also help to explain other peculiarities. Even the female plumage and the male nonbreeding plumage of *D. fusca* are less dull than those of many other warblers of the same genus. Their comparative brightness could also be adaptations to enhance flocks. Which would, in turn, tend to confirm the hypothesis that the role of the species in mixed flocks in winter quarters is of considerable biological significance, both to the species itself and to its associates. Possibly this sort of slightly ambiguous relationship is characteristic of many warblers that migrate to the neotropics. At least *Wilsonia pusilla,* also with bright female and male winter plumages, plays a not dissimilar role in the flocks of the mountains of western Panama (Moynihan, 1962c).

Atlapetes pallidinucha, in central Ecuador, seems to play much the same role as *A. rufinucha* in most other regions, which might help to explain why Ecuadorean *rufinucha* are somewhat aberrant.

The noisy and conspicuous flycatchers *Uromyias agilis* prefer bamboo and are usually nuclear, more passive than active, joined and followed more often than joining or following, but also interacting reciprocally with a variety of different partners in all directions with appreciable actual frequency. Thus they resemble *Hemispingus atropileus* in many effects and relations. As far as I could tell, however, they do not discourage or displace local *H. atropileus.* The two species seem to flourish side by side in this region. Doubtless their feeding habits are sufficiently different to permit coexistence (*Uromyias* probably is more consistently insectivorous). Possibly there are also slight differences in their social roles which are only revealed in special circumstances. The single good example of flock assembly at dawn that I was able to follow closely in this region was certainly centered on *H. atropileus.* A family group of this species was joined by a pair of *Myioborus melanocephalus;* the two species were joined by a pair of *Anisognathus igniventris;* and

TABLE 17

Mixed Flocks Along Road to Santo Domingo, ca. 2,805–2,683 m, March 1966

Hours of observation: 14 1/2
Average no. of individuals seen per hour: 15.03
Average no. of individuals seen in mixed flocks per hour: 8.62
Individuals seen in mixed flocks as % of total no. of individuals seen: 57.34%
Average no. of mixed flocks seen per hour: 1.31
Average no. of highly organized mixed flocks seen per hour: 0.41
Average no. of individuals seen per mixed flock: 6.58
Largest no. of individuals in one flock: 17
Average no. of species per mixed flock: 4.0
Largest no. of species in one flock: 10

then individuals and groups of other species came in, one after the other, in rapid succession, as a sort of social precipitation. It is still interesting that two species such as *Uromyias agilis* and *Hemispingus atropileus* can play such similar roles, nearly identical and frequently interchangeable in nonexceptional circumstances, in the same community and often with the same individual companions. Roles are more stable or at least less varied than are players.

The habit of forming mixed flocks is restricted in central Ecuador. The pattern of restriction may reveal some of the ultimate or intermediate term causal factors involved in the development of such behavior. Mixed flocks appear at ecological frontiers, but only certain kinds of frontiers. They *do not* occur at the borders between humid high altitude forest and scrub and either humid páramo (e.g., above San Juan) or relatively arid habitats at any elevation (e.g., south of Quito in the central basin). They *do* occur at the borders between high altitude humid forest and similar or more lush and complex humid (''upper subtropical'') vegetation at middle latitudes. The effect was observed along the road to Santo Domingo, below and to the west of San Juan. The relevant data are indicated in Tables 16 and 17. Mixed flocks, quite absent at higher elevations along this road, appear abruptly between 3,000 and 2,900 m. They are moderately well-developed from their first appearance. This is just the altitude at which strays from lower elevations begin to occur on occasion. Among the strays are the bright tanager *Anisognathus flavinuchus* and (again) the warbler *Basileuterus coronatus;* probably also the ''ivorybill'' woodpecker *Phloeoceastes pollens.* These species usually, or always, associate with flocks when they occur in the area. This might be expected of strays. More significant is the fact that mixed groups are formed in the area irrespective of whether or not any strays happen to be visible or audible at the time. The habit of forming mixed flocks may be, in part, an adaptation to cope with invaders; but it is not simply a direct response to their immediate presence (see, also, below).

Eastern Cordillera of Colombia

Species seen to be regular or frequent members of high altitude forest and scrub flocks.

TABLE 18
Mixed Flocks at Guasca, September 1962

Hours of observation: 10 3/4
Average no. of individuals seen per hour: 6.79
Average no. of individuals seen in mixed flocks per hour: 3.26
Individuals seen in mixed flocks as % of total no. of individuals seen: 47.95%
Average no. of mixed flocks seen per hour: 0.37
Average no. of highly organized mixed flocks seen per hour: 0.28
Average no. of individuals seen per mixed flock: 8.75
Largest no. of individuals in one flock: 16
Average no. of species per mixed flock: 5.50
Largest no. of species in one flock: 9

Brush-finches: *Atlapetes rufinucha, A. schistaceus; Atlapetes pallidinucha* also occurs, but seems to be rare or scattered in this region, at least in the areas in which I worked.

Bush-tanagers and bush-warblers: *Basileuterus luteoviridis, B. nigrocristatus, Chlorospingus canigularis, Cnemoscopus rubrirostris, Hemispingus atropileus, H. melanotis, H. verticalis;* probably also *Basileuterus signatus* and *Hemispingus frontalis.*

Bright tanagers: *Anisognathus igniventris, Buthraupis montana, Chlorornis riefferii, Dubusia taeniata, Iridosornis rufivertex, Tangara vassorii* (and other species of the genus, mostly green and black, *labradorides* and possibly *nigroviridis*), and *Thraupis cyanocephala.*

Honeycreepers: *Conirostrum albifrons, C. rufum, C. sitticolor;* perhaps *Diglossa cyanea* and others.

Whitestart: *Myioborus ornatus.*

Furnariids: *Synallaxis* spp., including *subpudica* and *unirufa.*

Tyrannids: *Mecocerculus leucophrys, Pyrrhomyias cinnamomea, Uromyias agilis,* and others.

Others: the cotingas *Pachyrhamphus versicolor* and *Pipreola riefferii,* the thrush *Turdus fuscater,* some wren(s), green toucanets, *Aulacorhynchus* sp. or spp. (probably *prasinus*), and the hummingbird *Coeligena torquata.*

Some of the dimensions of interspecific gregariousness in the region are

TABLE 19
Mixed Flocks at Guasca, April 1965

Hours of observation: 13 1/2
Average no. of individuals seen per hour: 12.81
Average no. of individuals seen in mixed flocks per hour: 4.81
Individuals seen in mixed flocks as % of total no. of individuals seen: 37.51%
Average no. of mixed flocks seen per hour: 0.75
Average no. of highly organized mixed flocks seen per hour: 0.30
Average no. of individuals seen per mixed flock: 6.50
Largest no. of individuals in one flock: 12
Average no. of species per mixed flock: 4.10
Largest no. of species in one flock: 6

TABLE 20
Mixed Flocks at Guasca, August 1965

Hours of observation: 7 1/4
Average no. of individuals seen per hour: 10.48
Average no. of individuals seen in mixed flocks per hour: 2.07
Individuals seen in mixed flocks as % of total no. of individuals seen: 19.74%
Average no. of mixed flocks seen per hour: 0.41
Average no. of highly organized mixed flocks seen per hour: 0.14
Average no. of individuals seen per mixed flock: 5
Largest no. of individuals in one flock: 8
Average no. of species per mixed flock: 4.33
Largest no. of species in one flock: 7

shown in Tables 18–24, which give counts of behavior in three areas, viz, below the Páramo de Guasca, on the mountains above Bogotá (primarily Guadalupe), and around Agua Bonita. Most of the counts were made in April or August 1965. The physiological conditions of the local birds were diverse during these periods. The eastern cordillera of Colombia has a complex climatic regime of two rainy and two less rainy seasons per year. The local birds have adapted to this regime in various ways. There are supposed to be two peaks of breeding activity, in March and in September–October, in most years (Olivares, pers. comm.). These coincide, more or less, with the first parts of the wettest seasons. Many species may breed twice a year. It is not certain that many individuals do.

There are also variations from year to year and site to site, and differences among individuals of the same and closely related species. Thus, for instance, male *Atlapetes schistaceus* uttered many advertising songs, presumably in courtship, at Guasca in April 1965, while neighboring *A. rufinucha* had almost stopped singing and was moving around with mates and fledged young. I have more numerous, but not more consistent, data on diglossas and conebills. Most honeycreepers were in full early breeding condition (much song and some nest building) at Guasca in September 1962; they were quieter, presumably advanced into incubation, a month later. They showed very few signs of breeding on Guadalupe or in the gardens of Bogotá in April 1965; but

TABLE 21
Mixed Flocks on Mountains above Bogotá, April 1965

Hours of observation: 21 3/4
Average no. of individuals seen per hour: 9.22
Average no. of individuals seen in mixed flocks per hour: 2.25
Individuals seen in mixed flocks as % of total no. of individuals seen: 24.26%
Average no. of mixed flocks seen per hour: 0.59
Average no. of highly organized mixed flocks seen per hour: 0.14
Average no. of individuals in one flock: 3.77
Largest no. of individuals in one flock: 7
Average no. of species per mixed flock: 2.77
Largest no. of species in one flock: 5

TABLE 22
Mixed Flocks on Mountains above Bogotá, August 1965

Hours of observation: 11 1/2
Average no. of individuals seen per hour: 12
Average no. of individuals seen in mixed flocks per hour: 4.52
Individuals seen in mixed flocks as % of total no. of individuals seen: 36.96%
Average no. of mixed flocks seen per hour: 0.87
Average no. of highly organized mixed flocks seen per hour: 0.52
Average no. of individuals in one flock: 5.10
Largest no. of individuals in one flock: 12
Average no. of species per mixed flock: 3.30
Largest no. of species in one flock: 8

some individuals, most of *D. l. lafresnayii* and *D. cyanea*, were singing frequently at Guasca at the same time. In August 1965, *D. cyanea, coerulescens,* and *lafresnayii* appeared to be coming into breeding condition at Guasca, while *D. carbonaria humeralis* was quiet; *D. cyanea* and *D. carbonaria humeralis* were singing on Guadalupe, while *D. lafresnayii* was quiet; and all *D. albilatera,* and possibly some *D. cyanea* and *D. coerulescens* were breeding at Agua Bonita. Finally and unexpectedly, there was little reproductive activity by honeycreepers of any kind on Guadalupe in September 1974.

Some conditions are more obviously "abnormal" than others. There was even more rain than usual for the season in and around Bogotá in April 1965. It has already been mentioned that much of the vegetation near Guasca was burned early in the same year. Such destruction of habitat must have had profound effects upon the local birds. This is one of the reasons why Table 18, a count made at Guasca in 1962 in the first stage of this study, is included in addition to later and perhaps more sophisticated counts. The 1962 figures may be more nearly typical of the area as it was at one time.

The eastern cordillera of Colombia is another intermediate region, in this context as in others. There is more interspecific gregariousness, on the whole or on the average, in this region than in central Ecuador or northern Peru, but less than in the extreme south of the cold humid zone in southern Peru or northern Bolivia—or in some other regions of the northern Andes (see

TABLE 23
Mixed Flocks at Agua Bonita, April 1965

Hours of observation: 8 1/4
Average no. of individuals seen per hour: 8.24
Average no. of individuals seen in mixed flocks per hour: 4.97
Individuals seen in mixed flocks as % of total no. of individuals seen: 60.29%
Average no. of mixed flocks seen per hour: 0.36
Average no. of highly organized mixed flocks seen per hour: 0.36
Average no. of individuals in one flock: 13.67
Largest no. of individuals in one flock: 26
Average no. of species per mixed flock: 8.67
Largest no. of species in one flock: 15

TABLE 24
Mixed Flocks at Agua Bonita, August 1965

Hours of observation: 13
Average no. of individuals seen per hour: 13.23
Average no. of individuals seen in mixed flocks per hour: 9.31
Individuals seen in mixed flocks as % of total no. of individuals seen: 70.35%
Average no. of mixed flocks seen per hour: 1.23
Average no. of highly organized flocks seen per hour: 0.85
Average no. of individuals in one flock: 7.56
Largest no. of individuals in one flock: 19
Average no. of species per mixed flock: 4.50
Largest no. of species in one flock: 11

below). More precisely, there are no suitable areas in the eastern cordillera that do not have some mixed flocks, but the local indices of gregariousness are never maximal.

Within the cold humid zone of the eastern cordillera, the largest flocks may occur at the lowest altitudes, e.g., Agua Bonita.

At their best, they are still smaller than the largest flocks of some other northern regions. They are also very discrete, often close together but seldom overlapping. They may overlap or come together less frequently than do the more widely ranging flocks of the central and western cordilleras of Colombia.

There is a more remarkable difference. As far as can be told in the admittedly difficult circumstances, mixed flocks are often or usually better developed in the breeding seasons than in the nonbreeding seasons in the eastern cordillera. This is not true of most other regions.

The particular social roles of given species, whenever they occur in mixed flocks, tend to be as conventional in the eastern cordillera as elsewhere, with the usual and expected scattering of minor exceptions. It was my impression that certain of the local diglossas, especially *D. carbonaria humeralis* and *D. l. lafresnayii* at higher altitudes, are more likely to "escort" groups in the eastern cordillera than are their closest relatives in most other regions. *D. coerulescens*, on the other hand, was never seen with flocks, nor were *Myioborus miniatus* or *Catamblyrhynchus diadema*. The last two forms seemed to be rare in this region. Perhaps I would have seen them join and follow other species had I been able to find them more often. The local representatives of *Basileuterus nigrocristatus* in the eastern cordillera may show a stronger predilection for bamboo thickets than do some other populations. They also sometimes appear to try to avoid flocks (going low and quiet while a group passes by) although not always with success. Much of the ordinary intraspecific social behavior of the species, conspicuous if not rigidly controlled, must make avoidance difficult.

The birds of large flocks in the eastern cordillera and other parts of the northern Andes utter a great variety of vocalizations. The ranges of sounds accompanying northern flocks seem to be broader, and perhaps more fluctuating, than the sounds of most Bolivian flocks. It is my impression that the loud rattles of *Basileuterus* and *Hemispingus* species are less often predominant in the north than in the far south (the shyness of some *nigrocristatus* must contribute to the result).

The occurrence of green toucanets in groups of finches, tanagers, honeycreepers, etc., is a noteworthy features of the eastern cordillera—toucans usually prefer one another—but it is not unique to the region.

At least one typical flock of small birds at Agua Bonita was followed by a single squirrel, doubtless *Sciurus granatensis* (Hershkovitz, 1947). This widespread mammal has a tendency to develop specialized interspecific relations of several kinds. It interacts with small monkeys, Rufous-naped Tamarins (*Saguinus geoffroyi*) and Squirrel Monkeys (*Saimiri sciureus*), in different ways in central and western Panama (Moynihan, 1976), and also associates with other bird groups in other parts of the northern Andes.

Sierra de Mérida

Species seen to be regular or frequent members of high altitude forest and scrub flocks.

Brush-finches: *Atlapetes albofrenatus,**[1] *A. schistaceus.*

Bush-tanagers and bush-warblers: *Basileuterus luteoviridis, B. nigrocristatus, Chlorospingus opthalmicus, Hemispingus goeringi,*** *H. reyi;* probably also *H. frontalis* and/or *H. superciliaris.*

Bright tanagers: *Anisognathus lacrymosus, Catamblyrhynchus diadema,** *Chlorophonia pyrrhophrys,**** *Dubusia taeniata,*** *Tangara vassorii, T. nigroviridis,* and *Thraupis cyanocephala.*

Honeycreepers: *Conirostrum sitticolor, Diglossa coerulescens,* and probably others.

Whitestart: *Myioborus ornatus.* (All or most of the individuals seen must have been examples of the form *albifrons.* This has been considered to be a separate species, but it is certainly closely related to *ornatus* populations to the west and south.)

Furnariids: *Margarornis squamigera, Synallaxis unirufa,* and several others (both woodhewers and spinetails).

Tyrannids: *Mecocerculus* sp., *Uromyias agilis,*** and several others.

Hummingbirds: *Coeligena bonapartei* (*eos*),** *C. torquata,* and others.

Others: the migrant Black and White Warbler *Mniotilta varia,** other warblers migrant from North America, the wren *Troglodytes aedon,* the brightly colored woodpecker *Piculus rivolii,** and a green toucanet *Aulacorhynchus* sp.*

Counts of flocks at Espejo (around and between La Montaña and La Aguada), La Negra, and Zumbador are shown in Tables 25–29.

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[1] Species marked with a single asterisk were seen in mixed flocks in this region only on Pico Espejo. Species marked with two asterisks were seen in mixed flocks only at Páramo Zumbador. Species marked with three asterisks were seen in mixed flocks only at Páramo La Negra. Some of them were also seen apart from flocks in other parts of the region and/or with flocks in other regions.

TABLE 25
Mixed Flocks on Pico Espejo, April 1965

Hours of observation: 23
Average no. of individuals seen per hour: 9.48
Average no. of individuals seen in mixed flocks per hour: 4.08
Individuals seen in mixed flocks as % of total no. of individuals seen: 43.12%
Average no. of mixed flocks seen per hour: 0.74
Average no. of highly organized mixed flocks seen per hour: 0.35
Average no. of individuals in one flock: 5.53
Largest no. of individuals in one flock: 16
Average no. of species per mixed flock: 4.06
Largest no. of species in one flock: 11

The interspecific gregariousness of the birds of the region is reminiscent of the eastern cordillera of Colombia, although it is probably somewhat greater on the average, despite obvious differences in species composition and climate (the mountains of western Venezuela must be very humid—note the scarcity or absence of *Anisognathus igniventris,* replaced by *A. lacrymosus* in most areas). The Sierra de Mérida also is intermediate for mixed flocks as well as for diglossas.

Most of the honeycreepers were in full early breeding phase at La Negra and on Espejo in September 1962. So were some finches and tanagers. There was much singing by many species in all areas visited in August and September 1965. It was evident, by contrast, that few of the common birds, with the probable exception(s) of *Thraupis cyanocephala* (and *Diglossa cyanea?*), were breeding in April 1965. As in the eastern cordillera, flocking seems to be better developed in the main breeding season than in the nonbreeding season. The climatic correlates may be different, however. According to the local people, the northern autumn is the least wet season in the Sierra de Mérida. Within any given season a short spell of rain or fog may tend to depress flocking in this region, but the impact is usually minor.

Leadership is clearer in the mixed flocks of the Sierra de Mérida than in the corresponding groups of some other regions, perhaps partly because bright tanagers are little varied in this Venezuelan outpost. Only *Anisognathus*

TABLE 26
Mixed Flocks on Pico Espejo, August–September 1965

Hours of observation: 14 1/2
Average no. of individuals seen per hour: 9.17
Average no. of individuals seen in mixed flocks per hour: 7.24
Individuals seen in mixed flocks as % of total no. of individuals seen: 78.95%
Average no. of mixed flocks seen per hour: 0.76
Average no. of highly organized mixed flocks seen per hour: 0.76
Average no. of individuals in one flock: 9.55
Largest no. of individuals in one flock: 22
Average no. of species per mixed flock: 5.91
Largest no. of species in one flock: 15

TABLE 27
Mixed Flocks at La Negra, April 1965

Hours of observation: 9 3/4
Average no. of individuals seen per hour: 8.31
Average no. of individuals seen in mixed flocks per hour: 2.87
Individuals seen in mixed flocks as % of total no. of individuals seen: 34.57%
Average no. of mixed flocks seen per hour: 0.61
Average no. of highly organized mixed flocks seen per hour: 0.31
Average no. of individuals in one flock: 4.67
Largest no. of individuals in one flock: 6
Average no. of species per mixed flock: 2
Largest no. of species in one flock: 2

lacrymosus and *Thraupis cyanocephala* were seen frequently, and the latter species tends to avoid flocks in the breeding season. The comparative insignificance of the bright tanagers throws the roles of the brush-finches, bush-tanagers, and bush-warblers into high relief. Such forms as *Atlapetes schistaceus, A. albofrenatus, Basileuterus luteoviridis,* and *Hemispingus reyi* are not only conspicuously nuclear here, but their "nuclearity" seems to be less ambivalent than that of their relatives in some other regions. The Venezuelan birds seem to be more often passive nuclear, joined and followed, and less often active nuclear, joining or following.

Atlapetes albofrenatus appears to be very closely related to *A. rufinucha,* which it partly replaces (perhaps another reflection of the great humidity of the region). Its ecological interactions with *A. schistaceus* remain obscure. I saw *A. albofrenatus* only on Espejo. Here most of the *A. albofrenatus* may prefer slightly lower altitudes than some of the *A. schistaceus,* but the two species overlap broadly. The two species often feed in the same places on the same or similar foods. They also sometimes occur in the same mixed flocks; but they probably do not usually associate with one another more closely than either does with members of flocks of different genera.

The local whitestarts and *Mecocerculus* flycatchers are scouts of the usual

TABLE 28
Mixed Flocks at La Negra, August–September 1965

Hours of observation: 11 1/2
Average no. of individuals seen per hour: 13.04
Average no. of individuals seen in mixed flocks per hour: 5.91
Individuals seen in mixed flocks as % of total no. of individuals seen: 45.34%
Average no. of mixed flocks seen per hour: 0.96
Average no. of highly organized mixed flocks seen per hour: 0.35
Average no. of individuals in one flock: 6.18
Largest no. of individuals in one flock: 15
Average no. of species per mixed flock: 3.25
Largest no. of species in one flock: 8

TABLE 29
Mixed Flocks at Zumbador, September 1965

Hours of observation: 8 1/4
Average no. of individuals seen per hour: 18.06
Average no. of individuals seen in mixed flocks per hour: 15.03
Individuals seen in mixed flocks as % of total no. of individuals seen: 83.22%
Average no. of mixed flocks seen per hour: 1.09
Average no. of highly organized mixed flocks seen per hour: 1.09
Average no. of individuals in one flock: 13.78
Largest no. of individuals in one flock: 22
Average no. of species per mixed flock: 7.67
Largest no. of species in one flock: 11

kind, but they seem to be followed more often than are their relatives and analogs in most other regions.

Diglossa coerulescens tends to keep apart from mixed flocks in most regions. It is usually much less friendly then *D. cyanea*, but it was found to be following groups on several occasions in several areas of the Sierra de Mérida. It may be a regular attendant here.

Basileuterus nigrocristatus sometimes tries to avoid mixed flocks; at other times it goes along with groups more or less happily, even showing or allowing special attachments (see below). The species is, therefore, more effectively nuclear in western Venezuela than around Bogotá. It may play the same roles in the Sierra de Mérida as in the southern Andes.

A very few green toucanets occurred in or near flocks on Espejo. I could not tell if the association was accidental or not.

Groups of the small bright "tanager" *Chlorophonia pyrrhophrys* were seen with mixed flocks at La Negra. Individuals of the species are very conspicuous and gregarious among themselves. I thought that their occasional approaches to other birds and flocks were partly coincidental. If they did play a special interspecific role, they can only have been irregularly nuclear.

The very different supposed tanager *Hemispingus goeringi* looks like another brush-finch of the *Atlapetes* proper type in the field. It is slatey above, rufous below, with prominent white eyebrows and long legs, and tends to move along or near the ground. I found it only at Zumbador where it associated particularly closely with *Atlapetes schistaceus* (see the contrast with *A. albofrenatus* on Espejo).

I saw a few other possibly significant associations of the same sort, i.e., pairs of species that stuck together for appreciable periods of time, apparently forming subunits within flocks. Among them were *Atlapetes schistaceus* and *Basileuterus nigrocristatus* on Espejo, *Anisognathus lacrymosus* and *Myioborus melanocephalus* on Espejo, and *Basileuterus luteoviridis* and *Margarornis squamigera* on Espejo and at Zumador.

Single squirrels, again *S. granatensis*, were seen with flocks several times in the Sierra de Mérida, usually following some yards behind, as occasional attendants in the conventional sense of the term.

SIERRA NEVADA DE SANTA MARTA

Species seen to be regular or frequent members of high altitude forest and scrub flocks (during my limited observations).

Brush-finch: *Atlapetes melanocephalus.*

Bush-tanagers and bush-warblers: *Basileuterus luteoviridis* and perhaps *B. basiliscus.*

Bright tanagers: *Anisognathus lacrymosus* (in the form of the distinctive *melanogenys,* sometimes considered to be a separate species), *Chlorophonia cyanea,* and *Thraupis cyanocephala.*

Honeycreeper: *Diglossa albilatera.*

Whitestarts: *Myioborus miniatus* and *M. flavivertex.*

Furnariids: a considerable variety; none securely identified as to species.

Tyrannids: *Mecocerculus leucophrys, Ochthodiaeta pernix,* and several others, almost certainly including the local form of *Pyrrhomyias cinnamomea.*

Hummingbirds: *Coeligena phalerata, Metallura tyrianthina,* and possibly one or two other species.

Others: the woodpecker *Piculus rubiginosus* and possibly a quail (*Odontophorus atrifrons?*).

A count of birds at San Lorenzo is shown in Table 30. The area is supposed to have two rainy seasons, in April–May and in September–November. My observations in August should have been in the "dry" season, but the area was actually wet at the time, with a great deal of rain and fog. Adults of several species were attended by fledged young.

Such as they are, the data indicate that interspecific gregariousness is rather well-developed.

The three most important nuclear species here are the endemics *Atlapetes melanocephalus, Myioborus flavivertex,* and *Anisognathus lacrymosus melanogenys.* Relations among them are asymmetrical; both the whitestart and the tanager seem to be more attracted to the brush-finch then to each other.

Atlapetes melanocephalus (a close relative of *A. rufinucha*) seems to fill much the same ecological niche as *schistaceus* in most other regions of the Andes, but it may have a slightly greater or more frequent preference for

TABLE 30
Mixed Flocks at San Lorenzo, August 1967

Hours of observation:	33 3/4
Average no. of individuals seen per hour:	9.36
Average no. of individuals seen in mixed flocks per hour:	6.49
Individuals seen in mixed flocks as % of total no. of individuals seen:	69.08%
Average no. of mixed flocks seen per hour:	0.83
Average no. of highly organized mixed flocks seen per hour:	0.44
Average no. of individuals in one flock:	7.82
Largest no. of individuals in one flock:	32*
Average no. of species per mixed flock:	4.43
Largest no. of species in one flock:	14

*This flock included a particularly large group of *Chlorophonia cyanea.*

bamboo. This last trait might help to explain why *Catamblyrhynchus diadema* is rare on Santa Marta. I saw it only once, and then apart from mixed flocks.

The endemic hummingbird *Coeligena phalerata* is a regular but usually brief and hurried visitor to mixed flocks. It resembles other members of the genus in this respect. Smaller *Metallura tyrianthina* is another visitor of the same general kind. The two hummingbirds do not associate with one another. They tend to avoid one another, visiting the same groups but seldom at the same times.

Males of the local *Diglossa albilatera* population are often persistent escorters. They show such behavior much more frequently than either females of the same species or both sexes of *D. carbonaria nocticolor*.

CENTRAL CORDILLERA OF COLOMBIA

Species seen to be regular or frequent members of high altitude forest and scrub flocks.

Brush-finches: *Atlapetes leucopis*,*[1] *A. rufinucha*, and *A. schistaceus*.

Bush-tanagers and bush-warblers: *Basileuterus luteoviridis*,* *B. nigrocristatus*, *Chlorospingus opthalmicus*,*** *Cnemoscopus rubrirostris*,* *Hemispingus atropileus*,* *H. superciliaris*, *H. verticalis*, and *Urothraupis stolzmanni*.**

Bright tanagers: *Anisognathus flavinuchus*,*** *A. igniventris*, *A. lacrymosus*, *Buthraupis eximia*,** *B. montana*,* *Catamblyrhynchus diadema*, *Chlorornis riefferii*,* *Dubusia taeniata*,** *Iridosornis rufivertex*, possibly *Tangara heinei*,*** *T. vassorii*, probably other *Tangara* spp., and *Thraupis cyanocephala*. Possibly, also, *Pipraeidea melanota*.

Honeycreepers: *Conirostrum albifrons* (white-capped), *** *C. sitticolor*, probably *C. cinereum*, and *Diglossa cyanea*.

Whitestarts: *Myioborus miniatus**** and *M. ornatus*.

Furnariids: *Synallaxis unirufa*, several other members of the same genus, and *Pseudocolaptes boissoneautii*.

Tyrannids: *Mecocerculus* sp.* (presumably *leucophrys*), *Ochthodiaeta* sp.,** *Ochthoeca rufipectoralis*, *Pyrrhomyias cinnamomea*,* and *Uromyias agilis*.

Hummingbirds: *Coeligena torquata*.

Others: *Pipreola* sp.* (presumably usually or always *riefferii*), a wren *Troglodytes solstitialis*,* several woodpeckers (at least *Veniliornis*, cf. *passerinii*,* and a *Piculus* sp.), a variety of migrant warblers, most notably *Dendroica fusca*.***

Plus squirrels.***

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[1] Species marked with a single asterisk were seen in mixed flocks in this region only on the eastern slopes of Puracé (Moscopán, Tijeras, etc.). Species marked with two asterisks were seen in such flocks only on the western slopes and at the edge of páramo on the same mountain. Species marked with three asterisks were seen in mixed flocks in this region only farther north, near Medellín, in and around Piedras Blancas, Santa Elena, Boquerón de Palmitas, La Montaña, and Belmira. Several of the same species were also seen apart from flocks in other areas.

TABLE 31
Mixed Flocks, Top and West (Popayán) Side, Puracé, May 1965

Hours of observation: 49 3/4
Average no. of individuals seen per hour: 8.56
Average no. of individuals seen in mixed flocks per hour: 4.02
Individuals seen in mixed flocks as % of total no. of individuals seen: 46.95%
Average no. of mixed flocks seen per hour: 0.68
Average no. of highly organized mixed flocks seen per hour: 0.42
Average no. of individuals in one flock: 5.88
Largest no. of individuals in one flock: 18
Average no. of species per mixed flock: 3.91
Largest no. of species in one flock: 10

Counts of interspecific gregariousness at these three series of sites in 1965 are shown in Tables 31–35.

The climatic regime of the region is at least as complicated as in the eastern cordillera. Local relief and wind patterns have various effects. There were hours and days of rain and hours and days of fine weather at all sites during all periods of counting. The rains were heavier and more frequent, on the average, on the eastern slopes of Puracé than on the western, and also greater in the southern part of the region than in those areas of the northern part in which I worked. What this really means in terms of seasons or biologically relevant parameters is difficult to say. My data on the subject are very imperfect. The local people have developed their own system(s) of classification. Thus, I was told, in August 1965, that it was simultaneously *verano* (presumably relatively dry) on the western slopes of Puracé and *invierno* (relatively wet) on the eastern slopes. I was told that July is relatively dry in the northern part of the cordillera (the heaviest rains usually stopping at the end of May or in early June). Trends in breeding behavior are somewhat easier to assess. Breeding seemed to be maximal on both slopes of Puracé in May 1965. Many individuals of all the local forms of diglossas and some hummingbirds, such as *Aglaeactis cupripennis* and *Colibri coruscans*, were in full song and courtship display. So were such birds as wrens, *Atlapetes* spp., *Anisognathus igniventris*, and *Myioborus ornatus*. At the same time

TABLE 32
Mixed Flocks, Top and West (Popayán) Side, Puracé, August 1965

Hours of observation: 7
Average no. of individuals seen per hour: 9.71
Average no. of individuals seen in mixed flocks per hour: 7.14
Individuals seen in mixed flocks as % total no. of individuals seen: 73.53%
Average no. of mixed flocks seen per hour: 0.57
Average no. of highly organized flocks seen per hour: 0.57
Average no. of individuals in one flock: 12.50
Largest no. of individuals in one flock: 22
Average no. of species per mixed flock: 8.25
Largest no. of species in one flock: 13

TABLE 33
Mixed Flocks, East (Moscopán) Side, Puracé, May 1965

Hours of observation: 19 3/4
Average no. of individuals seen per hour: 11.90
Average no. of individuals seen in mixed flocks per hour: 10.79
Individuals seen in mixed flocks as % total no. of individuals seen: 90.64%
Average no. of mixed flocks seen per hour: 0.91
Average no. of highly organized mixed flocks seen per hour: 0.81
Average no. of individuals in one flock: 11.83
Largest no. of individuals in one flock: 28
Average no. of species per mixed flock: 7.22
Largest no. of species in one flock: 16

I saw at least one adult *Atlapetes rufinucha* engaged in nestbuilding, and dependent begging young of several diglossas, of *Iridosornis rufivertex*, and of *Tangara vassorii*. Breeding was less intense or widespread at Puracé in August 1965, but by no means entirely suppressed in all cases. There were songs by *Diglossa cyanea*, *Dubusia taeniata*, *Atlapetes* spp., *Anisognathus igniventris*, and *Myioborus ornatus*, plus another nestbuilding performance by *Atlapetes rufinucha!* Many nectarivorous birds were obviously breeding in the northern part of the cordillera in July 1965, but there were few or no signs of reproductive activity among the tanagers near Santa Elena in November 1962.

Indices of interspecific gregariousness are high in the region as a whole. Breeding may discourage mixed flocking to some slight but significant extent in areas of sparse or degraded vegetation. In the lush forest of the eastern slopes of Puracé, however, there is little change in interspecific gregariousness from season to season. It is always strong in this area, during periods of maximal breeding as well as in periods of reduced breeding.

The counts in Table 35 are small and based upon a rather miscellaneous collection of birds and sites. They are inserted to show that flocking tendencies in the northern part of the central cordillera are of the same order of magnitude as in the southern part.

This more or less extreme gregariousness would seem to have developed

TABLE 34
Mixed Flocks, East (Moscopán) Side, Puracé, August 1965

Hours of observation: 13
Average no. of individuals seen per hour: 17.77
Average no. of individuals seen in mixed flocks per hour: 16.38
Individuals seen in mixed flocks as % total no. of individuals seen: 92.21%
Average no. of mixed flocks seen per hour: 1.08
Average no. of highly organized mixed flocks seen per hour: 1.08
Average no. of individuals in one flock: 15.215
Largest no. of individuals in one flock: 35
Average no. of species per mixed flock: 9.36
Largest no. of species in one flock: 28

TABLE 35
Mixed Flocks in the Northern Part of the Central Cordillera of Colombia, July 1965

Hours of observation: 23 1/2
Average no. of individuals seen per hour: 8.36
Average no. of individuals seen in mixed flocks per hour: 4.85
Individuals seen in mixed flocks as % total no. of individuals seen: 58.16%
Average no. of mixed flocks seen per hour: 0.64
Average no. of highly organized mixed flocks seen per hour: 0.55
Average no. of individuals in one flock: 7.60
Largest no. of individuals in one flock: 20
Average no. of species per mixed flock: 5.0
Largest no. of species in one flock: 16

in a straightforward way. Most of the species of the central cordillera play their usual social roles, only more frequently or vigorously. Even the exceptions and peculiarities are of the expected sorts.

A characteristic of the local flocks of the high altitude forest and scrub is hostile disputing. I saw more overt fights and chases among different species in the central cordillera than in most other regions. They were common on Puracé even in August 1965, which is past, or before, the peak of the breeding season. Here they usually involved members of the same flock.

Tangara vassorii and *Myioborus ornatus* seemed to be particularly aggressive. Perhaps their irritability was due to the crowding that is almost inevitable within large groups. Other encounters between honeycreepers and hummingbirds have already been described; some of them occurred in or near mixed flocks.

Hostility among members of the high altitude forest and scrub cluster may be as great here as in central Ecuador and greater than in the southern Andes, but it does not seem to discourage mixed flocking to the same extent as in Ecuador. Perhaps internal tendencies toward gregariousness are stronger here than in Ecuador (and the southern Andes?) and strong enough to counteract the effects of hostility.

There is crowding between as well as within groups. I noted more, or more extreme, overlaps of ranges among different flocks on the eastern slopes of Puracé and in the north of the central cordillera than anywhere else in the Andes, with the possible exception of Munchique in the western cordillera. I saw different mixed flocks pass within full sight and sound of one another, going in opposite directions but only a few hundred meters apart, without confusion. Sometimes a few birds switched from one group to another during a pass, but they usually did so neatly and quietly, with little or no indication of active hostility toward or from their new companions, and certainly less fighting than among individuals of a single flock in other circumstances.

Some of the mixed flocks near Santa Elena and in other areas of the northern part of the central cordillera were diffuse. Most of the Puracé flocks are concentrated. The difference may be related to densities of populations.

As in most of the Andes, the leadership of mixed flocks is shared among many species in the central cordillera (bright tanagers are not rare or insignificant here as in the Cordillera de Mérida). Such forms as *Basileuterus luteoviridis* are primarily passive nuclear here as elsewhere. With an unusual wealth of material to observe, however, I was impressed by the local importance of certain species that are less conspicuous to the human eye and ear in other regions. Thus, for instance, it was obvious in the central cordillera that irritable *Tangara vassorii* (ranging from high in trees to very near the ground), *Buthraupis eximia* (usually in trees), and *Synallaxis unirufa* (usually low) are often of great social weight and frequently are joined and followed by individuals of other species, and probably actually determine the courses of groups on many occasions. *Hemispingus verticalis* may be even more influential. The species is fairly abundant in the central cordillera. It is more arboreal than many other bush-tanagers and it is usually found high in trees. It tends to be restless and fast moving. Individuals of the species associate with one another, probably in family parties. I do not remember ever seeing an individual alone. Parties usually associate with other species in mixed flocks, often the largest flocks. Within mixed groups, *H. verticalis* is usually passive nuclear. It also, and this is not an inevitable consequence, tends to move in the forefront of the advance wave. It may be the nearest thing to a regular leader in the more high-flying sections of the mixed flocks of the central cordillera, joined and followed even more frequently than are *Buthraupis eximia* or *Tangara vassorii*. It certainly functions as a leader of mixed flocks more often in the central cordillera of Colombia than it does in the eastern cordillera.

The roles of *Atlapetes rufinucha* and of *A. schistaceus* are clearly differentiated on Puracé. In this region *A. schistaceus* is only moderately common. It seems to be largely or completely confined to wet forest and scrub on the eastern slopes. Here it is a conventional nuclear species of the usual Andean ambivalent or combined active-passive type. *Atlapetes rufinucha* extends over a wider area into relatively drier habitats. It is also more often purely passive nuclear, especially in thin or dispersed bush, e.g., hedges among crop fields. Pairs and family groups of the species tend to pursue their own ways quite determinedly. They seem to pay little attention to other birds. Simply because they do move vigorously and are conspicuous, however, they are themselves attractive to individuals of several other species. Doubtless their relative attractiveness is all the greater in dry and thin vegetation because such habitats are less crowded than areas of denser forest, and therefore contain fewer possible alternative foci, i.e., other species potentially capable of playing and supporting the passive nuclear role.

Local *A. schistaceus* may be partly restricted by competition from *Urothraupis stolzmanni*. Pairs and small groups of this "tanager" are rather brush-finch-like in habits and appearance. On Puracé they are common at high altitudes in dense scrub near the edge of páramo. This resembles some habitats favored by populations of *A. schistaceus* in southern and central Peru. On Puracé *U. stolzmanni* is often passive nuclear, obviously attractive to other species but not paying much visible attention to them. In this respect it is quite like nearby *Atlapetes rufinucha.*

The few *Atlapetes leucopis* that I saw in the central cordillera were moving near the ground in the same habitat, and sometimes the same flocks, as the *A. schistaceus.* They seemed to be playing roughly similar ambivalent nuclear roles. One pair of *A. leucopis* associated closely with a small group of *Synallaxis unirufa,* within a very large mixed flock, at irregular intervals over a period of at least several days. There was no evidence of any particularly close association between the two species of *Atlapetes,* apart from their occasional common membership in the same groups, along with other genera.

Local *Atlapetes rufinucha* certainly has special relations, but these are not usually with other finches. The species belongs to, and is often the leader of, a subset of the local cluster. The various species of the subset frequently tend to associate with one another, although not necessarily, or even usually, simultaneously. It is common to see two or three species of the subset together, perhaps any two or three species, but it is comparatively rare to see all of them together, at least apart from the largest mixed flocks that also include many other species that do not belong to the subset. Among the members of the subset, in addition to *Atlapetes rufinucha,* are *Myioborus ornatus, Anisognathus lacrymosus, Tangara vassorii, Diglossa cyanea,* perhaps *Basileuterus nigrocristatus* on occasion, and, at less than the highest altitudes, *Anisognathus flavinuchus, Thraupis cyanocephala,* and some other species of *Tangara,* most notably *heinei.* It probably is not coincidental that these birds are primarily black, yellow, and/or blue. The prevailing blue and yellow coloration may be compared and contrasted with the blue and buff or chestnut that is so conspicuous in the southern Andes (see, also, Moynihan, 1968a). The members of the subset of the central cordillera probably are brought together by both social and ecological factors, if, and insofar as, the two factors can be distinguished. They are among the relatively few species of the high altitude forest and scrub cluster that are likely to be abundant in semi-open vegetation. If they are to associate in mixed groups at all, they might as well pick one another. They will have no other choices in an appreciable number of circumstances.

Local *Conirostrum cinereum* are semi-commensals of man in gardens, hedges, and simplified scrub near villages. When they also associate with mixed bird groups they are most likely to join the black, blue, and yellow subset, even though their own coloration is different. *Dubusia taeniata* occurs in the same habitats, and is marked with blue, but it was seen in mixed flocks relatively less frequently. Similarities in color are not irresistible. They are suggestive rather than compelling.

Flocks are so large and common in some areas of the central cordillera that they encounter, and may appear to incorporate, elements that are extraneous. Thus, for example, I saw *Turdus fuscater* and *Atlapetes torquatus* close to members of flocks on Puracé. These associations were, I think, essentially coincidental. They were not prolonged.

Similarly, I saw two very small squirrels, *Microsciurus* (*alfari?*), with a mixed bird group at Boquerón de Palmitas. They remained behind when the flock drifted away. Several single *Sciurus granatensis*, on the other hand, seemed to be real followers or attendants of other mixed flocks near Belmira.

Mixed flocks are discouraged or suppressed and their members scattered by bad weather, e.g., heavy rain, in the central cordillera. They may be encouraged by mildly bad weather, such as light drizzle, or fog, or cloud. It was my impression that many groups encountered in fog were even larger than usual. Perhaps they were only noisier. In any case they were both active and coherent.

Western Cordillera of Colombia

In considering high altitude forest and scrub flocks, it may not be necessary to stress the distinctions between the northern and southern ends of this cordillera in the same way as in the discussion of the diglossa cluster. I saw fewer species in mixed flocks at Frontino than on Munchique, but the forms that were found in the north appeared to be, with some exceptions, a fairly representative sample of the range seen in the south. The difference was more quantitative than qualitative.

Species seen to be regular or frequent members of flocks in some or all parts of the region.

Brush-finches: *Atlapetes rufinucha, A. schistaceus, Oreothraupis arremonops,* and perhaps others.

Bush-tanagers and bush-warblers: *Basileuterus coronatus, B. luteoviridis, Chlorospingus canigularis, C. semifuscus, Cnemoscopus rubrirostris, Hemispingus atropileus, H. superciliaris, H. verticalis,* and probably others (e.g., an unidentified *Thlypopsis*).

Bright tanagers: *Anisognathus flavinuchus, A. lacrymosus, Buthraupis montana, Chlorornis riefferii, Dubusia taeniata, Iridosornis rufivertex, Tangara vassorii, T. xanthocephala,* other species of *Tangara*, and *Thraupis cyanocephala*.

Also *Piranga rubriceps*.

Honeycreepers: *Conirostrum albifrons "atrocyaneum," C. sitticolor*, plus several diglossas (at least *D. albilatera, D. cyanea*, and *D. carbonaria brunneiventris*) in different areas.

Whitestarts: *Myioborus miniatus* and *M. ornatus*.

Furnariids: Several spinetails, including *Synallaxis unirufa*, and a variety of larger arboreal types.

Tyrannids: species of *Mecocerculus* (at least *leucophrys*), *Pyrrhomyias cinnamomea*, and others (perhaps *Elaenia* sp. and *Myiotheretes fumigata*).

Hummingbirds: *Coeligena torquata, Ensifera ensifera*, and possibly several smaller forms (e.g., *Heliangelus exortis*).

Others: migrant warblers, vireo(s), small wren(s), *Pipreola arcuata*, woodpeckers (at least two species, one of them probably *Piculus rivolii*), and even thrushes of the genus *Turdus*.

Some counts of interspecific gregariousness at several sites in the western

TABLE 36
Mixed Flocks on Munchique in the Western Cordillera of Colombia, May 1965

Hours of observation: 29 1/4
Average no. of individuals seen per hour: 8.85
Average no. of individuals seen in mixed flocks per hour: 5.47
Individuals seen in mixed flocks as % total no. of individuals seen: 61.78%
Average no. of mixed flocks seen per hour: 0.72
Average no. of highly organized mixed flocks seen per hour: 0.48
Average no. of individuals in one flock: 7.62
Largest no. of individuals in one flock: 18
Average no. of species per mixed flock: 4.57
Largest no. of species in one flock: 13

cordillera in 1965 are shown in Tables 36–42. Most of the data were obtained in the Munchique area of the southern part of the cordillera, on the mountain itself, on the adjacent "spur" of San Gerardo–La Palma, and in the near vicinity of finca La Carpintería at the base of the mountain. Other counts were made in and above the station of Korea in the Farallones, also in the south, and just below the true páramo of the Frontino area in the north.

In most years there are heavy rains during April and May in the western cordillera. The Farallones were sopping wet when I made my count there in May 1965. As it happened, however, the weather was generally fine during the period of my counts on Munchique and at La Carpintería in the same month. This was an unusual bright interval; I was told that rains had been nearly continuous during the ten days immediately preceding the counts. August is supposed to be the middle of a "dry" season. There was still considerable rain during this month in 1965. Many birds of many different species and ecological types were in full breeding condition in the southern part of the cordillera in May 1965. Breeding behavior was somewhat reduced or less widespread in the same areas in August of the same year. Reproductive activity seemed to be nearly minimal at Munchique and west of Cali in November 1962. It was conspicuous at Frontino in July 1965.

Interspecific gregariousness among members of the high altitude forest and scrub cluster is obviously well-developed, strong, persistent, and extensive

TABLE 37
Mixed Flocks on Munchique in the Western Cordillera of Colombia, August 1965

Hours of observation: 18
Average no. of individuals seen per hour: 10.06
Average no. of individuals seen in mixed flocks per hour: 8.56
Individuals seen in mixed flocks as % total no. of individuals seen: 85.08%
Average no. of mixed flocks seen per hour: 0.61
Average no. of highly organized mixed flocks seen per hour: 0.56
Average no. of individuals in one flock: 14.0
Largest no. of individuals in one flock: 37
Average no. of species per mixed flock: 7.82
Largest no. of species in one flock: 19

TABLE 38
Mixed Flocks at San Gerardo-La Palma in the Western Cordillera of Colombia, August 1965

Hours of observation: 9 1/4
Average no. of individuals seen per hour: 8.32
Average no. of individuals seen in mixed flocks per hour: 5.07
Individuals seen in mixed flocks as % total no. of individuals seen: 61.04%
Average no. of mixed flocks seen per hour: 0.54
Average no. of highly organized mixed flocks seen per hour: 0.32
Average no. of individuals in one flock: 9.40
Largest no. of individuals in one flock: 20
Average no. of species per mixed flock: 5.0
Largest no. of species in one flock: 10

in the western cordillera of Colombia. For these birds and this kind of behavior, the western cordillera, probably in conjunction with the central cordillera, represents a northern extreme, comparable to the similar southern extreme in northern Bolivia and southern Peru, but very different from the opposite extreme in the intervening center, in parts of northern Peru and central Ecuador.

The mixed flocks of the western cordillera are often large and sometimes crowded together. I may have seen as many overlaps of flock ranges in the western cordillera as in the central cordillera.

Flocking is definitely stimulated by fog. This was most noticeable at La Carpintería.

As usual, leadership is varied and changeable. Most of the species that are occasional or intermittent leaders in other regions tend to play the same roles in the western cordillera. Only a few of the local forms appear to be slightly peculiar in that they are more, or less, influential here than elsewhere. *Cnemoscopus rubrirostris* is abundant in the western cordillera. Individuals of the species often associate with one another in groups of four to eight or more, which are probably extended families with allies and attachments. These groups are usually integrated into mixed flocks. When and if so, they tend to be conspicuously passive nuclear, much more frequently joined and

TABLE 39
Mixed Flocks near La Carpintería in the Western Cordillera of Colombia, April–May 1965

Hours of observation: 20 1/2
Average no. of individuals seen per hour: 8.15
Average no. of individuals seen in mixed flocks per hour: 6.88
Individuals seen in mixed flocks as % total no. of individuals seen: 84.43%
Average no. of mixed flocks seen per hour: 0.68
Average no. of highly organized mixed flocks seen per hour: 0.68
Average no. of individuals in one flock: 10.08
Largest no. of individuals in one flock: 20
Average no. of species per mixed flock: 6.15
Largest no. of species in one flock: 13

TABLE 40
Mixed Flocks near La Carpintería in the Western Cordillera of Colombia, August 1965

Hours of observation: 14 1/2*
Average no. of individuals seen per hour: 11.17
Average no. of individuals seen in mixed flocks per hour: 10.76
Individuals seen in mixed flocks as % total no. of individuals seen: 96.29%
Average no. of mixed flocks seen per hour: 1.10
Average no. of highly organized mixed flocks seen per hour: 1.04
Average no. of individuals in one flock: 9.75
Largest no. of individuals in one flock: 21
Average no. of species per mixed flock: 6.81
Largest no. of species in one flock: 15

*All observations were made in the afternoons, usually late, on five different days.

followed than joining or following. Thus the local populations of the species are gregarious both intra- and interspecifically. The combination recalls *Chlorospingus opthalmicus* of Chiriquí and, as noted above, is unusual in the humid cold zone of the Andes. Individuals and small or restricted family groups of *Tangara vassorii* also function as important leaders in the western cordillera, perhaps more peacably than in the central cordillera, with less overt aggression toward individuals of other species.

Hemispingus verticalis of the western cordillera, on the other hand, seems to be both less common and less attractive than it is in the central cordillera. It is more like its relatives in the eastern cordillera.

Iridosornis rufivertex of the western cordillera seems to be almost always passive nuclear.

It has already been mentioned that the interspecific roles of *Diglossa cyanea* and *D. carbonaria brunneiventris* are partially reversed in some areas of the northern part of the western cordillera. At moderate levels near Frontino *D. c. brunneiventris* is more often associated with mixed flocks, as an occasional attendant or active nuclear element, than is *D. cyanea.*

Pairs and families of *Conirostrum albifrons* "*atrocyaneum*" are more abundant, in appropriate habitats, in the western cordillera than are other

TABLE 41
Mixed Flocks in the Farallones in the Western Cordillera of Colombia, May 1965

Hours of observation: 17 1/2
Average no. of individuals seen per hour: 14.40
Average no. of individuals seen in mixed flocks per hour: 11.49
Individuals seen in mixed flocks as % total no. of individuals seen: 79.76%
Average no. of mixed flocks seen per hour: 1.26
Average no. of highly organized mixed flocks seen per hour: 0.91
Average no. of individuals in one flock: 9.14
Largest no. of individuals in one flock: 20
Average no. of species per mixed flock: 6.0
Largest no. of species in one flock: 13

TABLE 42
Mixed Flocks in the Páramo Frontino Region of the Western Cordillera of Colombia, July 1965

Hours of observation: 28
Average no. of individuals seen per hour: 10.61
Average no. of individuals seen in mixed flocks per hour: 7.78
Individuals seen in mixed flocks as % total no. of individuals seen: 73.40%
Average no. of mixed flocks seen per hour: 0.86
Average no. of highly organized mixed flocks seen per hour: 0.32
Average no. of individuals in one flock: 9.08
Largest no. of individuals in one flock: 24
Average no. of species per mixed flock: 5.21*
Largest no. of species in one flock: 14

*Based on 19 flocks.

populations of the species or superspecies in other regions of the Andes. I never saw them apart from mixed groups. They seem to be as nearly obligate commensals of flocks as are pairs and families of *C. sitticolor* everywhere. In flocks they behave in some of the same ways as *C. sitticolor*, but not always independently (see below).

Individuals and pairs of *Piranga rubriceps* were seen with several mixed groups in both the southern and northern parts of the western cordillera. They were usually fairly high in trees. They appeared to be functioning as attendants and probably are regular attendants. The genus *Piranga* is widespread in North America as well as in the mountains of Central and South America. The genus is brightly colored, but probably is not closely related to any of the bright tanagers listed or discussed above. There is red, pink, or orange in at least the breeding plumages of adult males of all forms of *Piranga*, but never any blue or bright green. Both adult male and female *P. rubriceps* are red, yellow, and black the year round. Different species of the genus have different interspecific reactions. The two forms resident in the mountains of Chiriquí, *P. leucoptera* and *bidentata*, seem to ignore mixed flocks. They occur in the vicinity of groups only casually or accidentally (pers. obser.). *P. flava* of southern Peru may not be much more gregarious (see above). Migrant *P. rubra*, by contrast, is a regular attendant, almost parasitic, upon mixed flocks in the lowlands of central Panama during the northern winter. It spends a great deal of time catching flying insects around the outskirts of groups; its local name is *come-abejas*, "bee-eater." My impression was that *P. rubriceps* of the western cordillera was doing little or no bee-eating or flycatching at the times of my observations. The two species may derive different benefits from their similar associations.

The mixed flocks of the western cordillera have rather vague borders. They may be vague in two senses.

At high altitudes the flocks on the average are so numerous and large that they often sweep up and temporarily incorporate individuals and groups of species that seldom or never occur in such mixed assemblages elsewhere in the Andes. Thus, for instance, I saw a large number of thrushes, *Turdus* *fuscater,* in or near mixed flocks in several areas of the western cordillera. They did not remain with the flocks for long, and the associations may have been partly accidental. The other members of the flocks seemed to be less disturbed by the presence of the thrushes than is usually the case in other regions. It may be that they had encountered them frequently enough to have become habituated. More remarkable were several visits to flocks, on Munchique and in the Farallones, by single individuals of the large, long-billed hummingbird *Ensifera ensifera.* This hummingbird is common throughout the length of the humid cold zone of the Andes. It usually avoids mixed groups except in the western cordillera.

Even brush-finches of the "*Buarremon*" type can be affected. I saw both *A. torquatus* and *A. brunneinucha* with mixed flocks in the southern part of the western cordillera, both simultaneously and separately. Twice, I found groups composed of four species of brush-finches, viz, *schistaceus, rufinucha, torquatus,* and *brunneinucha,* apparently without other companions (I do not know if other companions were present earlier). These were the most complex brush-finch flocks seen anywhere in the Andes in the course of this study.

Only a few species in the western cordillera seem to be impervious to the attractions of mixed flocks. Some of the resistent forms are highly gregarious among themselves. Groups of Acorn Woodpeckers, *Melanerpes formicivorus,* are common above La Carpintería, but they ignore and are ignored by the many mixed flocks of the high altitude forest and scrub cluster in the neighborhood. Similarly, groups of caciques, *Cacicus leucorhamphus,* pay little or no attention to the corresponding flocks of the Farallones.

In some parts of the western cordillera of Colombia, as at Machu Picchu in southern Peru and along the northern road to Santa Domingo in central Ecuador, there is fairly continuous seminatural vegetation from the borders of the high altitude grassland or moorland (páramo in Colombia) down to medium altitudes, 2,000 m and below. In such areas it is sometimes possible to observe contacts and interactions among species and flocks that are usually characteristic of different elevations. I saw examples of this in the Farallones and other hills west of Cali and Medellín.

A few species of "upper subtropical" facies occur at intermediate levels with otherwise "typical" high altitude forest and scrub flocks. Among these are such forms as *Myioborus miniatus, Basileuterus coronatus,* and *Tangara xanthocephala* (*Atlapetes brunneinucha* may fall into the same category). These species seem to play the same roles in mixed flocks at the upper limits of their ranges in the western cordillera as they do in similar environments and altitudes in other regions, or they exhibit the minor aberrations that might have been expected, granted the distinctive features of the western cordillera as a whole. Thus, *Tangara xanthocephala* is a particularly important leader, as is *T. vassorii.* Also, I have seen individuals of *Turdus serranus* swept into mixed flocks in much the same way as *T. fuscator* of higher areas.

Some *Myioborus miniatus* showed a tendency to stay nearer to the ground, in bushes and small trees, than did individuals of *M. ornatus* in the same flocks.

In all the regions in which it occurs, *Anisognathus flavinuchus* is most abundant at intermediate altitudes, below the densest concentrations of *A. igniventris* or *A. lacrymosus*. It also seems to prefer extremely humid areas; in this respect it is like *lacrymosus* but unlike *igniventris*. In many areas of the western cordillera it overlaps, or closely approaches, *lacrymosus* and can occur in the same or similar mixed flocks. Within flocks it tends to play the same ambivalent passive-active nuclear roles as its relatives. It is erratic and restless, making side forays, but it probably associates with flocks approximately as frequently as *lacrymosus* and more frequently than *igniventris*. The western cordillera of Colombia is one of the few regions of the Andes in which *igniventris* is very rare or absent. This is less likely to be a result of competition with *flavinuchus* than a consequence of the extreme humidity of the region and/or a reflection of the success of *lacrymosus*.

The specific composition of the avifauna changes below the "enriched" transitional zone. In humid forest and scrub at lower altitudes in the western cordillera the dominant flocks often include a core of several, perhaps as many as five or six, species of *Tangara* of different colors, (red, orange, and yellow, as well as blue and green). The leadership of *Tangara arthus* was conspicuous near Mares. Migrant warblers join these flocks in appreciable numbers, usually as attendants, at some times of the year. Most migrants seem to prefer relatively low and warm areas over the colder and more rigorous environments of higher altitudes.

I noticed a variety of special social relationships within the high altitude forest and scrub flocks of the western cordillera. They were usually too simple to be called subsets. Among the linked forms were *Cnemoscopus rubrirostris* and *Chlorospingus canigularis*, *Atlapetes rufinucha* and *Myioborus ornatus*, *Anisognathus lacrymosus* and *Diglossa cyanea*, *A. lacrymosus* and *Tangara vassorii*, *D. cyanea* and *Conirostrum albifrons* "*atrocyaneum*," and *C. a. atrocyaneum* and *Conirostrum sitticolor* (with or without *D. cyanea*). The relations between the conebills were interesting. On Munchique *C.a.* "*atrocyaneum*" tended to follow and join *C. sitticolor* repeatedly. The tendency was much less evident at Frontino.

It is conceivable that the distinctive coloration of adult male *C. albifrons* "*atrocyaneum*" is an adaptation to facilitate association with *D. cyanea* (see also the notes on Machu Picchu).

This brings up a point of some importance. The links among honeycreepers on Munchique are exceptional. So are occasional groups of mixed brush-finches. Other exceptions elsewhere in the Andes have been cited above. Such exceptions may be numerous in actual terms, but they are still relatively rare by comparison with other kinds of associations. As a general rule, when two or more species of the same genus or very similar ecological type occur in the same mixed flock, they do *not* associate with one another particularly closely, or at least any more closely than with other birds of other genera or types. They may, in a flock, perform many of the same activities in the same places. They do not usually do so at the same times. This indicates that they are carefully maintaining slight but definite social and physical distances among or between themselves, perhaps in the same way(s) as members of the diglossa cluster maintain greater distances in such regions as central Ecuador. The organization of mixed flocks must depend upon avoidance or repulsion as well as upon attraction. However, in flocks the attractions must be more far-reaching than the counteracting negative factors. All societies may depend upon the same forces, but the balance or equilibrium of forces must be different in different kinds of societies.

Single squirrels and even a few pairs of the usual species, *Sciurus granatensis*, were seen following mixed flocks of birds in the western cordillera, as elsewhere in the northern Andes. Squirrels seem to be comparatively abundant and easily visible in this cordillera, more so than in the other regions that I visited, and I had an opportunity to observe their behavior at some length. They were silent when associating with flocks although they can be noisy at other times.

In a previous publication (Moynihan, 1962c), it was suggested, in connection with Panamanian flocks, that the noisiness of the squirrels might enhance the conspicuousness, and therefore the attractiveness, of flocks. This would still appear to be plausible; but the effect may be deleterious in the Andes. Noise can be inappropriate or counterproductive in the wrong circumstances. One loud outburst of chattering by a solitary squirrel in the western cordillera was seen to attract thrushes. This is something that many members of a flock might want to discourage, or tend to be discouraged by. Thrushes may have to be tolerated in some flocks of the western cordillera, probably simply because they cannot be easily avoided in this region, but the behavior of most birds in other parts of the Andes indicates that all or most members of the genus *Turdus* are potentially disruptive to groups (see above). It must be assumed that squirrels derive benefits from joining and following flocks (otherwise they would not do so). It seems likely, therefore, that squirrels are silent while they are accompanying Andean flocks in order to avoid attracting the wrong kind of associates.

7

CONSIDERATION OF MIXED FLOCKS

The magnitude of the behavioral differences among associations of high altitude forest and scrub birds is very great. Interspecific gregariousness, as estimated by the indices listed in the tables in the preceding chapter, ranges from 0 to 96%, which is, of course, almost the full range possible. Indices and averages from many areas are summarized as graphs in Figures 11 and 12.

There is a faint suggestion, from the indices, that interspecific gregariousness increases or decreases by steps. This would not be surprising in theory. Some levels of sociability may be more stable or advantageous than others for purely social reasons, in any or all settings. Unfortunately, the available data are insufficient to prove or disprove the point; it should be remembered that the counts were made for purposes of illustration rather than statistical analysis. The most conspicuous step, the apparent gap between 0 and 12% gregariousness, could be an artifact. Intermediate levels might exist without being distinguishable from 0 or "random noise," by a human observer in the field.

The proximate causes of the formation of mixed flocks, the behavioral mechanisms involved, seem to be comparable in kind or quality to the corresponding factors controlling relations among species of the diglossa cluster, even though their actual expressions, immediate objectives and results, are different (or the reverse in some cases). Like the hostile or negative interspecific reactions between diglossas, the friendly or positive interspecific responses of numbers of mixed flocks probably are extrapolations of intraspecific behavior to wider social contexts or, in other words, to greater diversities of stimuli.

The maintenance of the extrapolations may be relatively easy for individuals belonging to populations such as those of *Cnemoscopus rubrirostris* of the western cordillera of Colombia and of *Chlorospingus opthalmicus* of Chiriquí, both of which show intraspecific as well as interspecific gregariousness. On the other hand, it must be less easy for individuals of populations and species that are not normally gregarious among themselves or at least are not gregarious as adults or apart from their families.

The last phrase is a clue to the origin of the responses. No matter how solitary an individual bird or mammal may be during most of its life as an adult, it still must be prepared to cope with a mate and perhaps young during the breeding season. It must also have been part of a family group, however small or temporary, when it was young. There are a few partial exceptions, e.g., some of the megapodes described by Frith (1962), but these are specialized situations and do not invalidate the general rule. Family patterns can be expanded in the course of evolution. It seems likely that *intra*specific gregariousness is one extension of family behavior (Ewer, 1968); intermediate

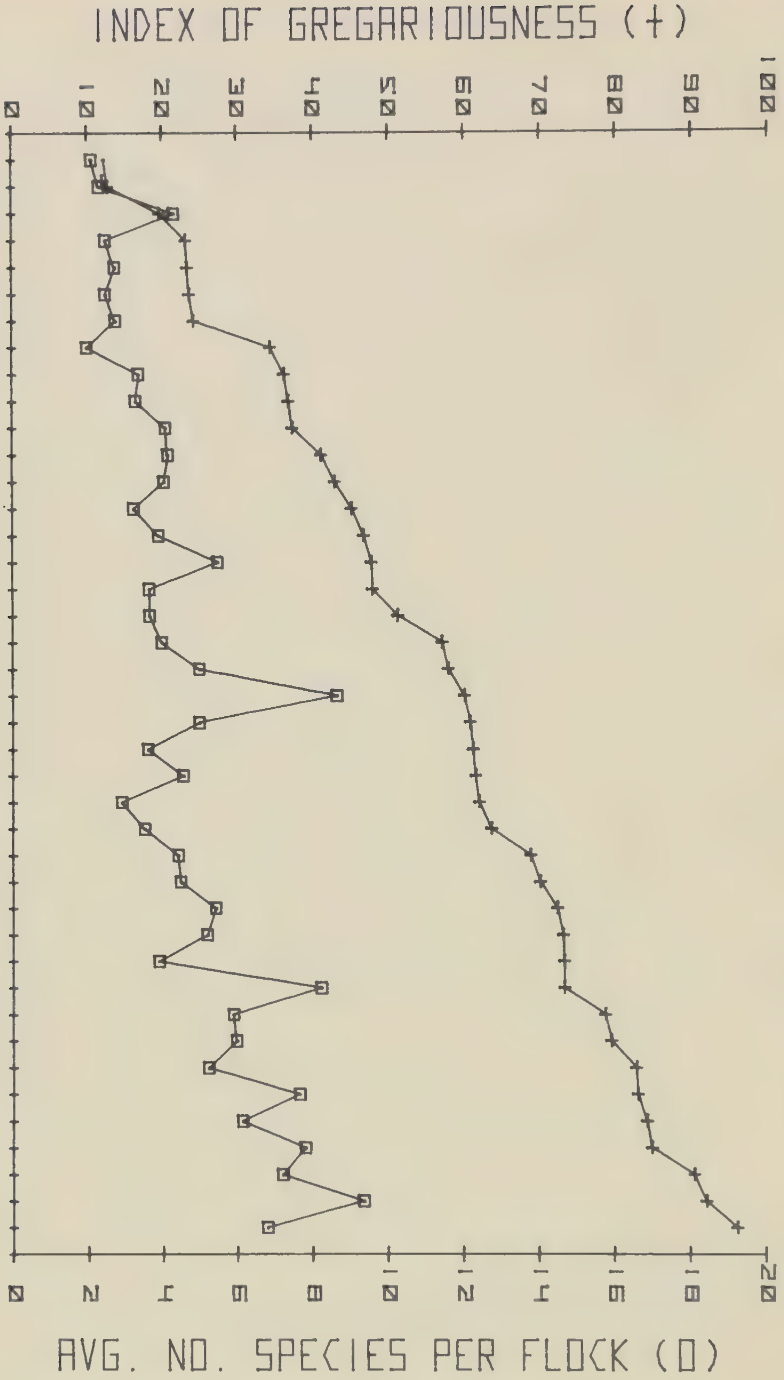

FIG. 11. Graph summarizing counts in areas in which mixed flocks were seen. Indices of gregariousness are plotted, from minimal to maximal, from left to right along the top line. The corresponding (per point) average number of species per mixed flock are plotted along the bottom line.

This and the remaining figures were prepared by D. Windsor.

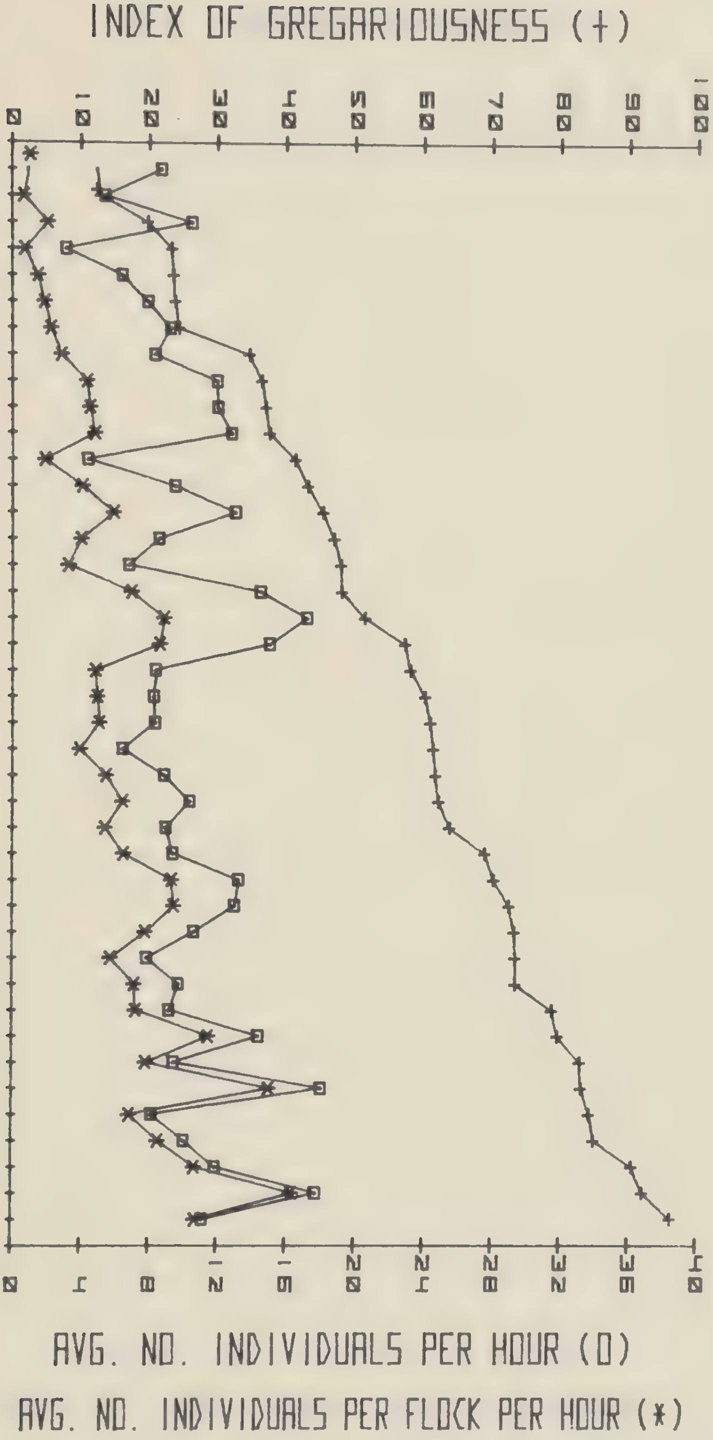

FIG. 12. Graph summarizing counts in areas in which mixed flocks were seen. Indices of gregariousness are compared with average number of individuals seen per hour and average number of individuals seen in mixed flocks per hour.

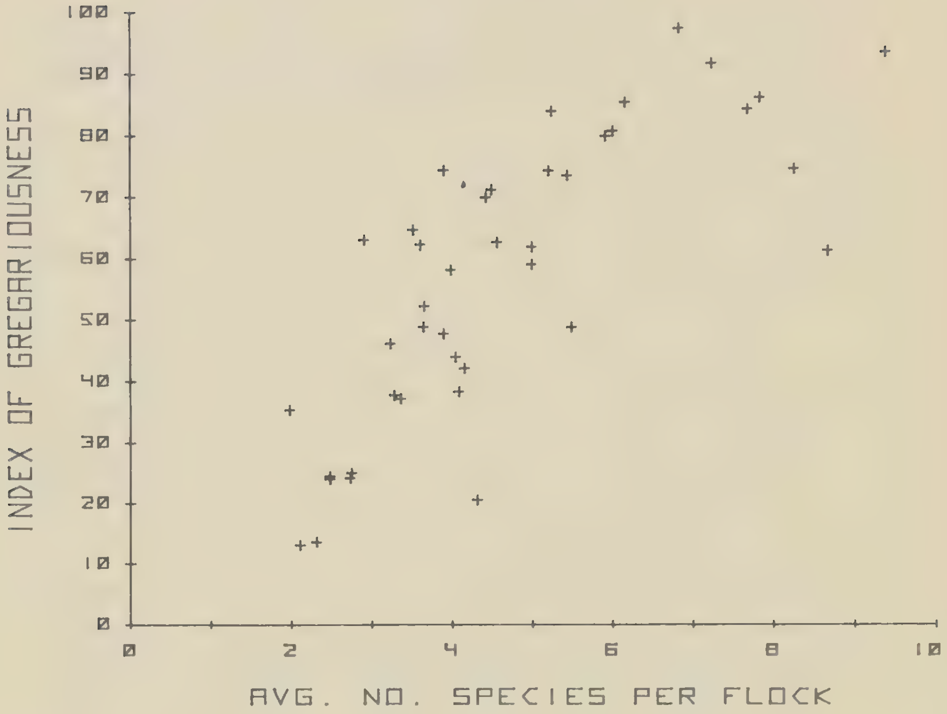

Fig. 13. Scatter diagram showing linear correlation between indices of gregariousness and average numbers of species per mixed flock. Correlation coefficient (rs) = 0.77. $p < 0.01$.

stages are known. There is no obvious reason why *inter*specific gregariousness could not have evolved from the same source, either directly or indirectly.

Remote causes of mixed flocks are ecological in the broad sense of the term. They also are reminiscent of the diglossa cluster in some respects but are rather different in others.

Within any given region of the Andes there are correlations between flocking and features of the environment, such as climate and vegetation. Mixed flocks tend to be largest and most elaborate in the local areas that have the densest and most diversified plant cover of more or less natural aspect, from tall trees to low shrubs. Note that dense vegetation favors increased contact among members of the high altitude forest and scrub cluster instead of decreased contact as among members of the diglossa cluster. The development of vegetation must be partly dependent upon climate. Direct effects of fog and rain upon flocking behavior have been mentioned. They are both various and localized. Similar atmospheric conditions can evoke different responses by the same or similar birds in different regions. Some correlations are better than others. None can be applied "across the board" to explain all the observed trends in behavior over the whole of the humid cold zone. The crucial factor here, as in the diglossa cluster, is the non-coincidence

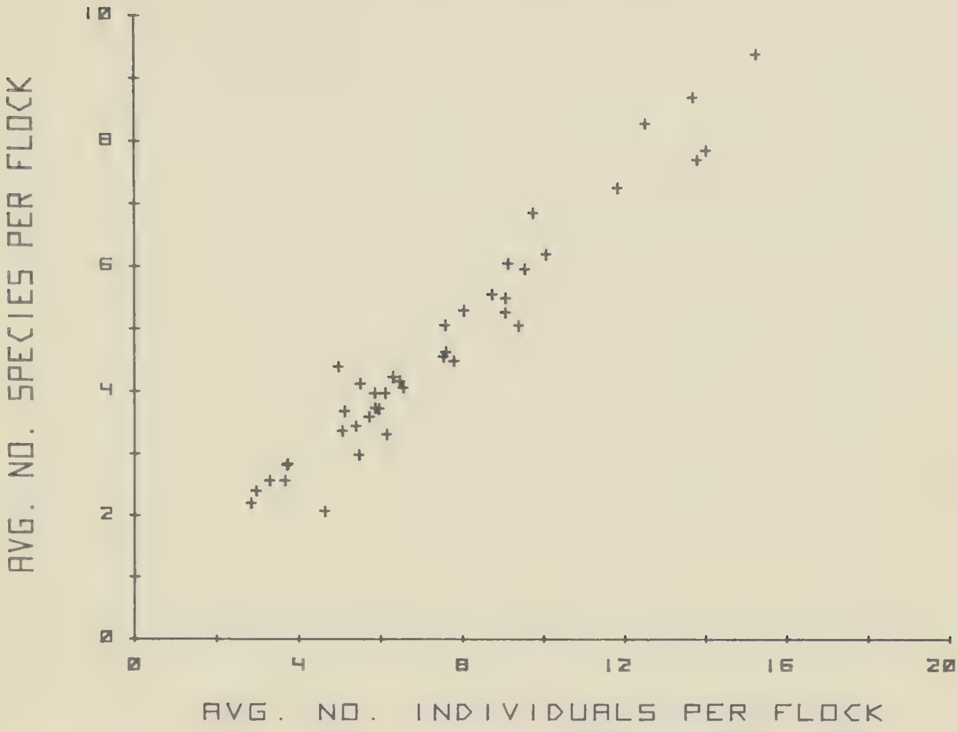

FIG. 14. Linear correlation between average numbers of species and average numbers of individuals per mixed flock. $rs = 0.97$. $p <<< 0.01$.

of distributions. The large scale trends of change in environmental parameters seem to be roughly unidirectional, proceeding from north to south or vice versa. The trends in flocking behavior are double, with the changes from south to center being the reverse, or mirror image, of the changes from center to north—both ends against the middle.

One would expect flocking to be correlated with the number of individual birds, and perhaps species. This may be true. At least the scatter diagrams of Figures 13 and 14 indicate that linear correlations between indices of gregariousness (essentially mixed flocks seen) and individuals counted and species distinguished are both positive and statistically significant, considering all (and only) the areas (points) in which mixed flocks were found or were recognized.

The results are not easy to interpret by themselves. The connections could be described in different ways. Mixed flocks may tend to be encouraged by increases in numbers of individuals and species. It is also probable that observations of species and individuals are facilitated by increases in the number of flocks, simply because large groups are more likely to be noticed than small ones. Both effects may have contributed to the appearance of the scatters in Figures 13 and 14. In any case, there seem to be exceptions and anomalies. Some of them may be real.

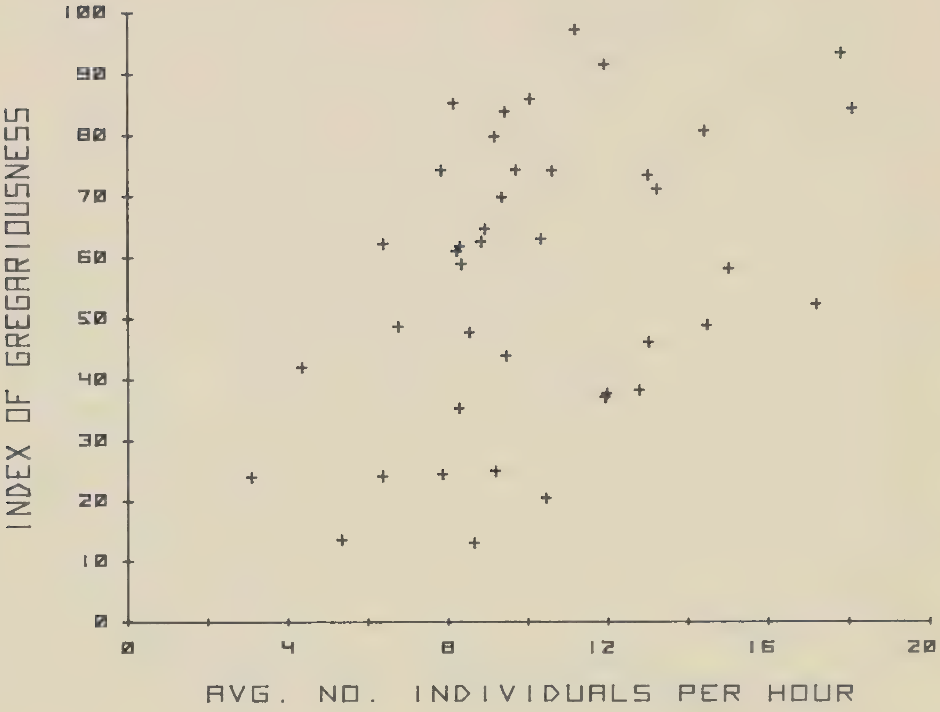

Fig. 15. Linear correlation between indices of gregariouness and average numbers of individuals seen per hour. $rs = 0.40$. $p = 0.01$.

The relative abundance of mixed flocks or frequency of flock formation can hardly depend to any very substantial extent upon numbers or diversities of species in whole regions even though there may be significant correlations among these factors for particular areas within regions. There are many more species of "flockable" types per region of the humid cold zone in the north of the Andes than in the south. A rough count of possibly relevant species listed in de Schauensee (1966) and Niethammer (1956) suggests that the difference could be of the order of 2 to 1. This is more than I found in most of the areas in which I worked. Perhaps relatively more species are rare or have restricted ranges of less than an entire region in the north than in the south. As far as I can tell, the number of species in the central Andes is intermediate. Thus, the trend in species number per region does not seem to coincide with the trends in interspecific flocking behavior any more closely than do the presumed gradients of climatic and vegetational changes.

The greater numbers of species in the north may be ascribed, in part, to the form of the "archipelago" in which they occur. The islands of the humid cold zone of the northern Andes are numerous and grouped together in a clump. They must present many favorable opportunities for multiple

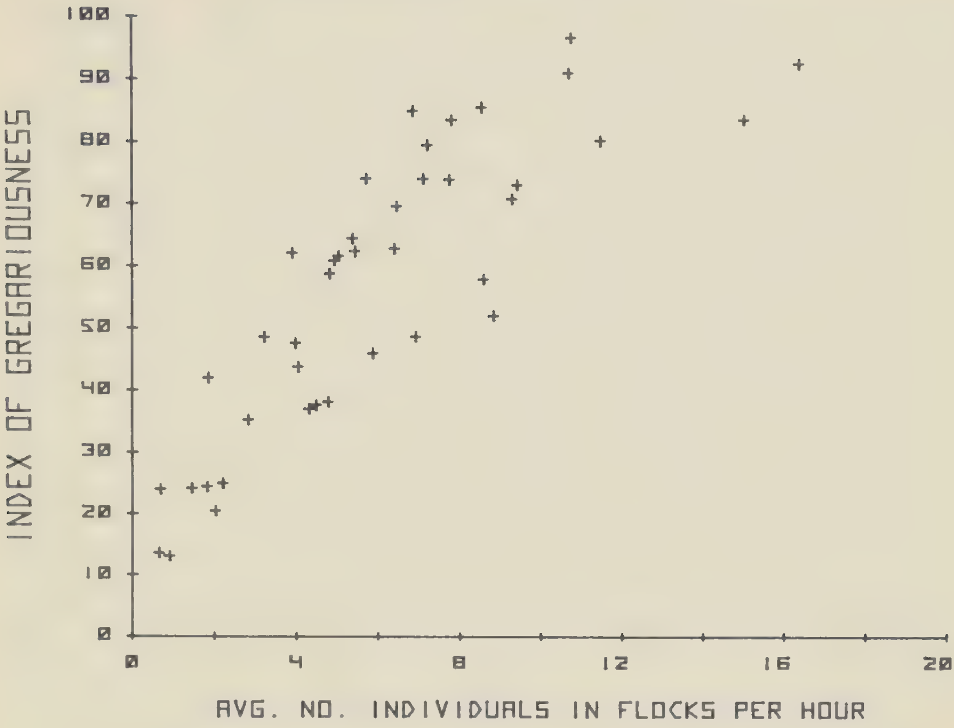

FIG. 16. Linear correlation between indices of gregariousness and average numbers of individuals seen in mixed flocks per hour. $rs = 0.84$. $p << 0.01$.

invasions and geographic speciation (see Mayr, 1942 and 1963), even more opportunities than the comparable regions of the southern Andes which are strung out in a single chain.

It would be foolhardy to try to estimate average numbers of individuals per unit area per region from our incomplete information. Doubtless the differences among them also conform to the environmental gradients. There is, however, a simple treatment of the available data that is suggestive. Ignoring intermediate regions and areas without flocks, the majority of the counts can be assigned to three categories: the far south, northern Bolivia, and southern Peru (Tables 1 through 7, pp. 94–102); the far north, the central and western cordilleras of Colombia (Tables 31 through 42, pp. 124–133); and what might be called the far center, extreme northern Peru (Cutervo) and central Ecuador (Tables 12 through 17, pp. 107–113). Looking at the scatter diagrams in Figures 15 and 16, which refer to average numbers of individuals seen per hour and in flocks per hour, and plotting regression lines upon them, it is possible to compare points above the lines (greater than the mean) with points below the lines (smaller than the mean). It will then be seen that the points below the lines outnumber the points above the lines in the central Andes, while the points above the lines outnumber the points below the lines in the far north and the far south. The differences, contrasting the center with the north and south together, are statistically significant by Fisher's Exact Probability Test ($p = 0.003$ for the average number of individuals seen per hour, and $p = 0.012$ for the average number of individuals seen in mixed flocks per hour).

This is encouraging support for the hypothesis, derived from qualitative observations, that there are real differences in the social behavior of the individuals concerned, differences that are in some sense intrinsic, apart from or in addition to the immediate effects of varying densities of populations. The birds of the central Andes do behave differently from their relatives to the north or south. There is real variation in gregariousness per se.

The geographic arrangement of different kinds of social behavior in the high altitude forest and scrub cluster, the dichotomy of north plus south versus center, is reminiscent of, although not absolutely identical with, the arrangement of hostile and avoidance behavior in the diglossa cluster. This suggests that the development of flocking is also partly dependent upon the sizes of regions. Or, probably more precisely, that it depends upon some aspects of competition that are themselves related to size or extent of regions. If so, given the differences among the reactions involved, the effects are not likely to be transmitted to the two clusters in the same ways. There is evidence that the relevant competition may be different for the two clusters.

Some of the advantages and disadvantages of associating in mixed groups are obvious and have been mentioned above and in many previous studies of the subject. Another possible advantage is less obvious and does not seem to have been discussed before. It may be general and crucial. The fact that members of flocks sometimes have to share resources may be said to increase competition among them. On the other hand, the fact that they are inevitably close together in space must reduce the probability that any one of them will be able to monopolize a resource. This works to even out the competition and to keep it within strict limits. The principle should apply to all flocks, of one or many species, if not always equally strongly in every case (see below). For many flocking birds it may be advantageous to tolerate or even encourage the relatively little competition that association in mixed groups may entail in order to avert a worse result. Not only may a member of a mixed flock obtain compensation in the form of increased access to food or better protection against predators, but it can also monitor its competitors to ensure that they do not make or exploit new advances, discoveries, or inventions on their own. Share and share alike, and every sharer may gain.

I think that factors of this sort must be invoked to help explain some of the peculiar features of the distribution of flocking, most notably the increase of gregariousness near the lower borders of the humid cold zone, where strays from the next lower humid zone begin to appear. It is easy to see why an invader might find it useful to join old established inhabitants. The problem is why the old inhabitants should allow it to do so. They may have little choice; perhaps an invader could be repelled only by fighting, which might be dangerous or ruinously expensive. But some of the birds of border areas seem to do more than accept strangers. Their conspicuous interspecific gregariousness must be positively inviting. Evidently it is adaptive for them to make special efforts to incorporate invaders. The differences between the gragarious tendencies of border birds and those of the same species in nonborder areas are a measure of the magnitude of the efforts. They do not seem to be small. Perhaps only a need to regulate the disposition and (re)partitioning of resources could justify the expenditure of time and energy.

It is also interesting to consider the central cordillera of Colombia. Members of the high altitude forest and scrub cluster behave in an extreme ‘‘northern way’’ in this cordillera, like their relatives and analogues in the western cordillera of Colombia. Members of the diglossa cluster do *not* behave in an extreme northern way in the central cordillera. The behavior of the local diglossas is variable and intermediate and rather strikingly different from that of their relatives in the western cordillera. The central cordillera is the largest region of discordance between the two clusters. One would like to know why. Probably the central cordillera, with other islands of the humid cold zone on all sides, east and west, as well as north and south, is particularly exposed to invasions from other highland birds flying over lowland gaps, as well as from lowland birds moving upward.

These facts reveal several differences between the two clusters. In both clusters there is a rough correlation between interspecific behavior and the sizes of regions. In both, interspecific behavior seems to be an adaptation to interspecific competition. Differences in the behavior of members of the same cluster in different regions seem to reflect different intensities and frequencies of competition. At this point the parallel stops.

Judging from the behavior of members of the diglossa cluster, their most important interspecific competitors are their usual neighbors. But invading strangers are the most important or dangerous interspecific competitors of members of the high altitude forest and scrub cluster.

The size of regions is significant for members of the diglossa cluster because it determines the total number of all competitors that they may meet. It is significant for members of the high altitude forest and scrub cluster primarily because it is linked to the relative extent of boundary areas through which many invaders must pass.

Some of the behavior of birds in mixed flocks, e.g., the sharing of food and the broadcasting of warning signals, are acts of the kind that has been called altruistic when performed by other animals in other circumstances (see, for instance, references in Wilson, 1975). I hope that the evidence and arguments presented here have shown that such patterns can be of immediate benefit to the performing individual itself, not only to its genes, and only indirectly to its family. Fortunately, kin selection can be largely ignored in discussions of mutual aid between individuals of different species.

Morse (1970) believes that mixed flocking among North American insectivorous birds (titmice, chickadees, nuthatches, creepers, kinglets, warblers) is negatively correlated with densities of populations and, inferentially, abundance of food. The worse the habitat, the better the flocks or the more advantageous the habit of associating in mixed groups. This could not be said, without many qualifications, of the mixed flocks of the higher Andes, or probably of other tropical environments. Interspecific gregariousness within the regions of the humid cold zone of the Andes is certainly positively correlated with densities of populations, at least in part or on the average, and the geographic variation between regions adds another dimension of complexity. It is suggestive, nevertheless, that in many regions of the Andes mixed flocks are better developed during the nonbreeding season than during the breeding season. Again inferentially, it may be assumed that food is less abundant during the former periods than during the latter. Perhaps the only generalization that could be applied to almost all mixed flocks of different continents and climates is that they are most likely to be formed, or to become large, when food or other resources are particularly difficult to find or use, because these resources are in short supply, because competition for them is intense or dangerous, or for some other reason. This is about as vague a generalization as could be devised. It could still be true.

A passage from an earlier paper (Moynihan, 1962c:120) may be quoted:

> "Granted that gregariousness is often advantageous in one way or another (as it obviously is), why do more species occur in mixed flocks than in unmixed flocks of their own species alone (apart from family groups)? Unmixed flocks might be easier to form and maintain, and might provide certain other social advantages that are lacking in mixed flocks. The answer to this question is probably that the members of an unmixed flock often compete with one another too strongly. . . . Association with other individuals of other species in mixed flocks may provide most of the advantages that could be obtained by association with other individuals of the same species in an unmixed flock, without the disadvantages of membership in an unmixed flock."

In retrospect, that passage seems a little oversimple, especially if the habit of associating in groups can help to restrict or to control competition. Individuals of the same species probably do tend to compete with one another more strongly, persistently, or precisely than do individuals of different species, even very similar forms. The implication to be drawn is that flocking is less frequently advantageous or effective as a regulator of the close competition among individuals of the same species than of the less close or consistent competition among individuals of different species.

Several other points may be noted in passing. There are often two or more species of the same genus in mixed flocks of the Andes. *Hemispingus*, *Atlapetes*, *Anisognathus*, *Basileuterus*, and *Tangara* provide examples. Such connections may be more common among neotropical birds than was originally supposed when fewer flocks had been studied. Different species of the same genus probably tend to compete less strongly than members of the same species, but more strongly than species of different genera. Intrageneric competition would appear, in many cases, to be serious enough to need regulation but not too serious to be regulated effectively by mixed flocks. It will be remembered that different species of the same genus, although they frequently occur in the same flocks, do not usually keep together or form a subset within a flock. The presence of other birds of other genera may be a useful social buffer.

Species that show intraspecific gregariousness, and therefore occur in large groups of their own species, might be expected to enjoy a competitive advantage in invading new areas or islands over stretches of unsuitable habitats. This is because, presumably, they would often arrive in a group, including several individuals capable of mating with one another. It is remarkable, therefore, that there are so few populations of this type in the insular areas of the high Andes at the present time. The high altitude forest and scrub cluster seems to be an association of considerable age (*vide* the social mimicry and other specializations of some of the components). Existing populations may be rather different from their ancestors, the first settlers. Their gregariousness may have changed with time; perhaps usually in one direction. Many settlers may have been gregarious among themselves when they first arrived in an isolated region but were then subjected to selection pressure against intraspecific gregariousness after they had become established. This might account for some of the differences between Andean flocks and the presumably younger flocks of southern Central America.

The suggested drift of change would effect patterns and sequences of invasions. A population that has just occupied a new island or region should be preadapted to invade others, while a population that has not moved recently might well lose its powers. Invasions may sweep in waves or epidemics, like pathogens. The longer the stay in a host region, the more likely a potential invader is to lose its ''virulence'' or ability to ''infect'' other regions. This is because it will become progressively more finely adapted to a particular set of conditions, and because its social behavior may change in such a way as to reduce the probability of new movements being successful.

8

CONCLUSIONS

DIFFERENCE BETWEEN THE TWO CLUSTERS

Members of the high altitude forest and scrub cluster are more or less friendly toward one another. Members of the diglossa cluster are basically unfriendly. The difference between the clusters is consistent despite all the variations within each.

The consistency cannot be a simple consequence of anatomy or physiology, much less of habitat preference. The two clusters occur in the same areas and environments. The members of the high altitude forest and scrub cluster are diverse. Some are high-flying, conspicuous, and perhaps extremely vulnerable to predation (Buskirk, 1976). Others skulk in low vegetation and are less exposed. Some resemble or overlap members of the diglossa cluster in size and patterns of activity. Some are closely related to diglossas phylogenetically.

The choice of foods may be a more relevant distinction. Feeding habits and social patterns are often causally linked. There may be some partial exceptions in a few groups of animals (Moynihan, 1976), but the statement holds as a general rule. Among Andean birds the linkage is apparent in both intra- and interspecific social relations. Most of the members of the high altitude forest and scrub cluster are insectivorous and/or frugivorous. Gregariousness is common among birds of such habits almost everywhere, not only in the Andes. Mixed flocks may be more common than unmixed flocks, but even the latter are not rare. Most of the members of the diglossa cluster are largely nectarivorous. Many nectarivorous birds are notoriously aggressive, either or both intra- and interspecifically. This is as true of the Old World Nectariniidae and the Australasian or Pacific honeyeaters of the family Meliphagidae (see, for instance, Ripley, 1959 and 1961) as of many honeycreepers and most hummingbirds (see papers cited above and their bibliographies).

The conebills and populations of *Diglossa cyanea* that associate with mixed flocks are less frequently or thoroughly nectarivorous than are other honeycreepers.

Again it may be supposed that intraspecific patterns and tendencies were selected for extrapolation when interspecific behavior was elaborated.

There must be a reason for the correlation between nectarivory and hostility. Nectar-bearing flowers do not seem to be more clumped, or more evenly dispersed, than many insects, small fruits, or edible buds. The various resources are not, however, renewable or replaceable in the same ways or at the same rates. A small fruit or an insect that is eaten is gone for food. There is no point to guarding or cultivating whatever remains may be left. A consumer can only look for more fruits or insects. A flower that is tapped for nectar, on the other hand, is not necessarily destroyed in the process. If it is allowed to survive it may produce more nectar in the near future. It is worth protecting. This may be sufficient to tilt the balance of selection pressures in favor of overt defense and aggression or, in certain circumstances, the development of some other specialized system, such as mutual avoidance and inhibition, to restrict the number of rivals at any given point at any given time.

Of course, there is often some minor hostility mixed with the friendliness of members of the high altitude forest and scrub cluster. Probably all social relationships include some hostile components. In the regions where hostility within this cluster is somewhat greater or more overt than usual, the increase may be related to crowding or, in central Ecuador, to a relaxation of pressure in favor of gregariousness, rather than to a change of food habits. Not all similar phenomena are due to precisely the same causes.

NATURE OF COMPETITION AND THE SIGNIFICANCE OF CLUSTERS

Although it is convenient to speak of competition among species, the phrase is another abbreviation. The real competition is among individuals. It can take a variety of forms. Many recent studies have shown that competition among vertebrates and perhaps other animals is usually strongly ''personal.'' The personal aspect seems to characterize both direct and diffuse competition, among individuals of different species as well as among individuals of the same species.

In theory individuals should be able to compete with one another simply by appropriating resources, without paying any particular attention to one another. This does not seem to be common among tropical vertebrates. Most tropical birds, many mammals (diurnal primates and squirrels), and coral reef fishes obviously do pay close attention to many of their neighbors, again of both the same and different species (not just potential predators and parasites). In most cases they also respond socially to several different kinds of neighbors. Members of the Andean clusters are quite conventional in these respects. The joining and following responses of members of the high altitude forest and scrub cluster are as personal as the attacks by members of the diglossa cluster.

Interspecific clusters have been noticed more frequently in the tropics than in the temperate zones of North America or northern Eurasia. They may be more abundant or varied in the tropics than elsewhere, or perhaps only more conspicuous.

A few comments in the Introduction should be repeated and stressed. Clusters are real entities. Some individuals and species can belong to more than one cluster. The majority do not. Most of them react to some of their neighbors in more specialized ways than they do to others. Clusters do not intergrade smoothly and imperceptibly. Social boundaries and gaps exist.

There may be general advantages to a cluster system in addition to the particular advantages provided by or derived from the special reactions within a cluster that hold it together or distinguish it as such. Interactions among the members of a cluster are rather stereotyped, in a given area or set of conditions, at least in extreme regions if not always in intermediate ones (see p. 88). The same specialized patterns tend to be applied to all representatives of a particular category, e.g., accepted foreigners, irrespective of species. Their release and orientation often appear to be semiautomatic. These features must favor speed of response, reduce hesitation, and help to avert confusion. There is an analogy. At different levels of social behavior clustering, the the ritualization of signals must have similar or parallel effects and uses.

Known clusters seem to be designed to be invasion resistent. Some of the interspecific behavior patterns of members of clusters are adapted to impede or eliminate new competitors directly or immediately. The mere existence of interspecific conventions, whatever their nature, could also be discouraging in itself. Even an invader that was ecologically compatible with a local cluster, in feeding habits and other requirements, might still be chivied or harassed by the local residents if it did not conform to the local social arrangements.

For many tropical birds the establishment of satisfactory relations with their neighbors must be among the most important adaptations to their environments. For invaders, social adjustments may have first priority. Dispersal ability may depend as much on social mobility as on powers of flight.

The habit of clustering, insofar as it may determine the number and qualities of individuals and species present, must affect the levels of resource utilization in an area. It may have recondite effects as well as obvious ones. Diamond (1975) has recently produced an interesting ecological and geographical classification of the birds of New Guinea and adjacent islands. He distinguishes "high-S species confined to the most species-rich islands," several classes of tramps that extend to progressively more species-poor islands, and "supertramps, confined to species-poor islands and absent from species-rich islands." He also suggests that high-S species have an overexploitation ethic, that they may exclude competitors by reducing resource levels to below the point where invaders can survive. The members of the diglossa and of the high altitude forest and scrub clusters of the Andes would appear to be generally comparable to the high-S and better class (less trampish) tramps of Diamond's classification. (They all seem to be the results of "K-selection" in MacArthur-Wilson terminology.) I think that it is possible, however, that the Andean forms may be underexploiting more frequently than they are over-exploiting. They certainly can be very abundant in many regions, but they also, at least in the northern parts of the Andes, manage to accommodate fairly substantial numbers of migrants from North America for several months of most or all years. On the very incomplete evidence available it could be argued that the members of the Andean clusters, with their special social reactions to repel invaders and/or space out and regulate competitors, are often failing to utilize all the resources that could be extracted from their surroundings. Behaving in this way, apparently self-denying, they may be able to preserve resources for occasional periods of scarcity and stress. Restraint may be effectively prudent. Localized and territorial as most of these birds are most of the time, the practice of conservation should be advantageous for any individual and its descendants, perhaps even other kin, in the long run.

9

SUMMARY

This paper is concerned with the behavior and ecology of certain birds of the humid cold zone of the tropical Andes.

The zone, from approximately 2,400 m to 3,600 m, extends from western Venezuela to Bolivia. Within these limits its distribution is complex and eccentric. There are isolated or insular areas in the north and semi-isolated, semi-insular or peninsular, areas in the south. The natural vegetation of the zone would be dense forest and scrub. Some of this may survive with modifications. Much of it has been destroyed, to be replaced by crop fields, hedges, gardens, etc. New patches of rich and sometimes exotic vegetation have been provided by irrigation, plantations, and other human activities.

The birds that were studied occur in natural-looking forest and scrub. They have also occupied some of the man-made habitats.

They can be assigned to two clusters of species: (1) honeycreepers of the genus *Diglossa* and a few relatives, as well as competitors or collaborators and (2) some frequently associated tanagers, finches, warblers, honeycreepers, flycatchers, furnariids, dendrocolaptines, woodpeckers, and others.

Members of each cluster react to other members of the same cluster in specialized ways (this is the definition of a cluster). Reactions may be negative or positive. Both are social.

Many species of the two clusters show pronounced *intra*specific geographic variation in *inter*specific behavior.

Most of these behavior patterns and the variations thereof seem to be adaptations to different kinds and degrees of interspecific competition, direct or diffuse, probably for many resources, including resting places, lookout posts, protective cover, escape routes, nesting sites, and even time or opportunity to communicate, in addition to food.

The characteristic interspecific reactions within the diglossa cluster are hostile, aggressive, or aversive.

In the main central mass of the tropical Andes, in central Ecuador and apparently northern Peru west of the Marañón valley, individuals of several different species of the cluster have broadly overlapping territories and habitat and food preferences, but they are usually kept apart at any given moment by an elaborate system of social segregation, without fighting. The segregation is supplemented by mutual and reciprocal inhibition of songs.

Individuals of the same and similar species in the southern part of the western cordillera of Colombia exhibit what might be called "extreme northern" behavior. Here the various species are kept apart from one another by different habitat preferences and a system of microgeographical separation. The separation may be inforced by fighting. Reciprocal inhibition of songs is not often necessary except in a few cases.

The two systems intergrade in other regions of the northern Andes. There is almost every conceivable intermediate between social segregation and microgeographical separation. Social relations between species can be untidy, with frequent encounters, intermittent fighting, and breakdowns of inhibitions. Complexity, confusion, and variability are maximal in the central and eastern cordilleras of Colombia.

Trends are reversed in the southern third of the humid cold zone. There are many overlaps and contacts among members of the cluster in central and southern Peru, somewhat mitigated or modified by an emphasis on interspecific territoriality. Neat and clean microgeographical separation reappears in northern Bolivia, the southernmost region visited.

The contrast is between the north and south together, on the one hand, and the center, on the other hand.

The characteristic interspecific reactions within the second cluster are friendly. Members of this cluster show greater or lesser tendencies to associate with one another in mixed species flocks.

The general distribution of gregariousness is clear, despite considerable differences between closely adjacent sites, variations from time to time at the same site, and miscellaneous apparent exceptions and anomalies. Mixed flocks tend to be very large, elaborate, and persistent in the western and central cordilleras of Colombia. They are usually smaller and simpler, perhaps briefer, in other parts of the northern Andes. They are even rarer and less developed in Ecuador and are absent from the most central area. They increase again in central Peru, and reach another climax of size and elaboration in southern Peru and northern Bolivia. As in the diglossa cluster, the basic pattern is dichotomous or trichotomous. The north and south resemble one another, and both differ from the center.

The species that may occur in mixed flocks are exceedingly diverse. Some of them range high in the treetops; others remain low in scrub and understory. Some are primarily insectivorous, catching small arthropods in different places in different ways. Many are semiomnivorous. Some are primarily frugivorous, taking different fruits, seeds, and other vegetable materials by different methods. A few are partly nectarivorous, although probably less so than most members of the diglossa cluster. Different species must be deriving different mixes of advantages from their associations with and in flocks.

Groups of birds in the northern Andes are often accompanied by squirrels, *Sciurus granatensis*.

Few of the birds of Andean flocks are gregarious intraspecifically, as well as interspecifically.

There are several kinds of social roles within mixed flocks. In the Andes it is possible to distinguish between nuclear and attendant forms, and between regular and occasional members. Most of the nuclear species can be either or both active (following and joining) or passive (followed and joined) according to circumstances. The relevant circumstances differ from species to species. A species may play a different assortment of roles in different areas. The same assortment can be played by different species in the same or different areas. Roles may be more stable or less varied than players.

The specialized interspecific reactions of members of both clusters probably originated as extrapolations of intraspecific activities. It may be a general rule that interspecific behavior does not usually entail new outputs or the performance of new patterns, but rather a receptivity to new inputs and a (re)classification of them in the central nervous system of the receiver, and thus a willingness to perform old patterns in new contexts.

Both the expressions of hostility or aversion in the diglossa cluster and of gregariousness in the flocking cluster are related to many aspects of the immediate environment, most notably climate and density of vegetation and all their dependent variables. Flocking is also positively correlated with the number of individuals and, less closely, the number of species present at any given point.

These relations would be expected. They cannot, however, explain all the differences in interspecific social behavior within either of the two clusters. There is a residue of differences that needs to be explained in other terms. At a superficial level, the terms should be geographical.

The humid cold zone of the tropical Andes is divided into different regions. The regions differ in size. The main central mass is large. The northern insular regions are smaller; some are fragmented; some are more isolated than others. The southern semi-insular, or peninsular, regions are also smaller, probably progressively smaller with increasing distance from the center.

Some of the differences in interspecific behavior seem to be related to sizes of regions.

In the diglossa cluster the largest region is characterized by social segregation; the smallest regions are characterized by microgeographical separation; and the intervening regions are intermediate. In the cluster of potentially gregarious species the largest region shows the least flocking, while the smallest regions show a great deal of flocking.

The geographical parameters are important because they determine the numbers and kinds of competitors of other species that an individual may have to cope with.

For members of the diglossa cluster it seems to be worthwhile to fight competitors in small regions, bringing about microgeographical separation, simply because the total number of possible opponents (per region, not just at a single point) must also be relatively small. The number of potential opponents must be larger in large regions. In these conditions, the risks of fighting probably would be prohibitively great, and it should be more advantageous to be tolerant. Social segregation with reciprocal inhibition is a compromise, a system of tolerance that may also limit competitors by restricting their movements and communications. The limitation is partial, but doubtless better than nothing.

Some of the obvious benefits and drawbacks of associating in mixed flocks have been known for a long time. Observations of Andean flocks suggest that there is another less obvious advantage. The fact that members of flocks sometimes have to share resources may be said to increase competition among them. The fact that they are inevitably close together in space must reduce the probability that any one of them will be able to monopolize a resource. Thus, even friendly flocking may be an adaptation to monitor and, implicitly, control competitors. Again this is a compromise partial solution.

Many interactions among different species in mixed flocks are of the kinds that have been called altruistic when performed by other animals in other contexts. They can also be selfish. They cannot, in these particular cases, be due to kin selection.

Despite the overall similarities, variations in interspecific behavior are not completely concordant or parallel in the two Andean clusters. Details of distribution would seem to indicate that the nature of the most important or dangerous competitors is different for birds of different clusters. Members of the diglossa cluster are evidently concerned with total numbers of competitors of other species; but members of the flocking or flockable cluster of high altitude forest and scrub habitats seem to be most preoccupied by a special class of competitors, i.e., invaders from other zones and regions, especially from lower altitude forest and scrub.

Variation within a region is revealing. Flocking is more highly developed near some frontiers than in nonfrontier areas of the same region. The more developed flocks are found in areas where strays from other zones appear with appreciable frequency, but they are found, or at least are maintained, even when strays are not present at the moment. The increase of gregariousness may be an adaptation to strays; it is not a reaction to them.

The same factors, on a different scale, may help to explain the connection between flocks and sizes of regions. The relative proportion of frontier to nonfrontier area varies, of course, with the size of the inner area. A larger proportion of the resident population will be exposed to invaders in a small region than in a large region. It is easy to understand, therefore, why flocking as an adaptation to control competing invaders should be more favored in a small region than in a large one.

The flocking birds of the central cordillera of Colombia appear to be anomalous in that they are more gregarious than would be expected from the rather large size of the region. Perhaps the central cordillera is particularly exposed to invasions, over gaps in this case, because it is surrounded on all sides by other "islands" of the humid cold zone.

The social differences between the two clusters are correlated with feeding. The most relevant aspect of food may be renewability. In many cases a flower that is tapped for nectar can survive to produce more nectar in a few hours or days. It is worth protecting. An insect or small fruit usually is consumed entirely. There is little or nothing left to protect. Nectarivorous birds tend to be less friendly, more defensive, often aggressive, than are insectivorous or frugivorous species almost everywhere, not only in the Andes.

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